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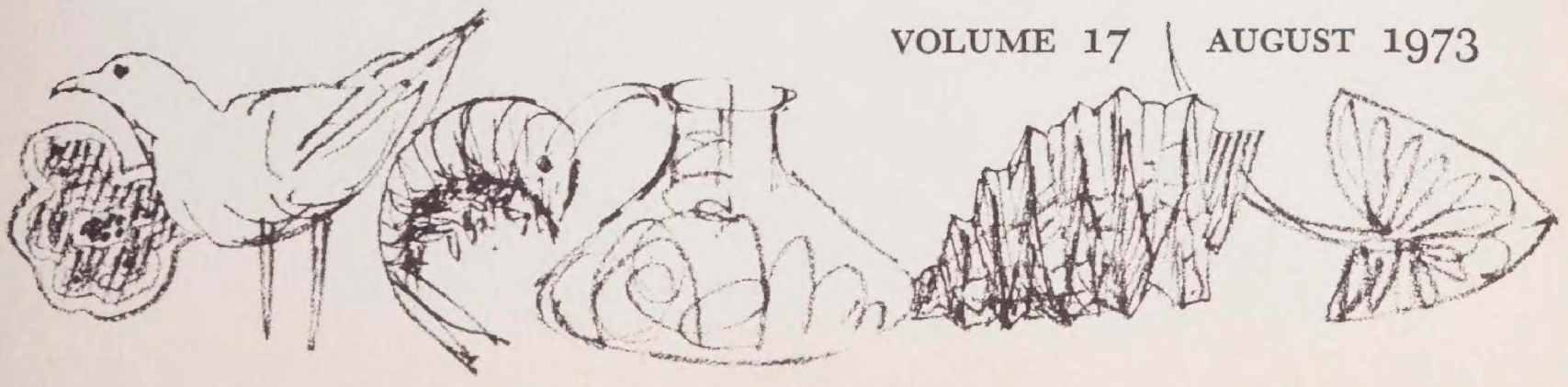

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Contents

Instructions to Authors iii

Caloric Values of Marine Animals from the Gulf of Mexico. *Thomas E. Wissing, Rezneat M. Darnell, Mohamed A. Ibrahim, and Leo Berner, Jr.* 1

Effect of Salinity on Acute Toxicity of Mercury, Copper, and Chromium for *Rangia Cuneata* (Pelecypoda, Mactridae). *Karen R. Olson and Richard C. Harrel* 9

Benthic Marine Algal Ecology in the Port Aransas, Texas area. *Peter Edwards and Donald F. Kapraun* 15

The Effect of Temperature and Swimming Speed on the Oxygen Consumption of Two Snappers, *Lutjanus campechanus* (Poey) and *Rhomboplites Aurorubens* (Cuvier). *Richard H. Moore* 53

A Trawl Study of Nearshore Fishes and Invertebrates of the Georgia Coast. *H. Dickson Hoese* 63

Observations on the Hydrology and Marine Organisms of the Tidal Colorado River and Adjacent Waters, Texas, February–June, 1962. *Richard A. Diener* 99

Tropical and Temperate Stranded Seeds and Fruits from the Gulf of Mexico. *Charles R. Gunn and John V. Dennis* 111

Corpus Christi Pass: A Hurricane Modified Tidal Inlet on Mustang Island, Texas. *Richard A. Davis, Jr., W. George Fingleton, Gerald R. Allen, Jr., Charles D. Crealese, William M. Johanns, Joseph A. O'Sullivan, Catherine L. Reive, Sandra J. Scheetz, and Gary L. Stranaly* 123

A Key to Unbranched, Cylindrical Brown Algae. *Michael J. Wynne*..... 133

A Gradient Apparatus for the Study of Salinity Preference of Small Benthic and Free Swimming Organisms. *Richard K. Keiser, Jr. and David V. Aldrich* 153

The Relationship Between the Pituitary Content of Prolactin and Blood Sodium Levels in Mullet (*Mugil Cephalus*) Transferred from Sea Water to Fresh Water. *Martin Sage* 163

Galveston Bay Benthic Community Structure as an Indicator of Water Quality. *J. S. Holland, Nancy J. Maciolek and C. H. Oppenheimer* 169

CALORIC VALUES OF MARINE ANIMALS FROM THE GULF OF MEXICO[1]

Thomas E. Wissing[2], Rezneat M. Darnell,
Mohamed A. Ibrahim, and Leo Berner, Jr.

Departments of Oceanography and Biology, Texas A&M University, College Station, Texas 77843

ABSTRACT

Caloric values are presented for forty-three groups of marine organisms from the Gulf of Mexico. The planktonic invertebrates averaged 5052, benthic invertebrates 4487, and fishes 5572 cal/gm ash-free wt. Among the invertebrates highest caloric values were exhibited by those forms which are passively planktonic, and the lowest values were observed in the benthic species, bubble floaters, and active swimmers. Larval fishes gave higher values than did the adults. Ash weights tended to be highest in the benthic forms.

INTRODUCTION

Considerable interest now centers around the study of energy flow through ecological systems, and efforts are currently being made to proceed beyond the analysis of primary productivity to assess the flow of energy through the consumer species. In carrying out energy studies of the consumer levels of the community, one of the first steps involves the determination of caloric equivalents so that standing crop data for individual species may be expressed in terms of calories. Published tabulations of caloric data (Golley, 1961; Slobodkin and Richman, 1961; Cummins and Wuycheck, 1971) provide equivalent values for a variety of freshwater and terrestrial species, but relatively few for marine forms. However, recent studies on the bio-energetics of marine ecosystems have resulted in a growing literature dealing with the caloric content of marine organisms derived largely from coastal and nearshore habitats (Vinogradova, 1961; Vinogradova, *et al.*, 1962; Paine, 1964; Ostapenya, 1966; Comita, *et al.*, 1966; Pandian, 1967; Pandian and Schumann, 1967; Brawn, *et al.*, 1968; Paine and Vadas, 1969; Petipa, *et al.*, 1970; Clutter and Theilacker, 1971).

Despite this recent interest, published data on caloric values of marine animals are still quite scarce, and this is especially true for offshore marine animals. To aid in filling this void and to provide some basis for interpreting the energy content of marine animals, in general, we present herewith a preliminary list of caloric values for animals derived from a series of nearshore and offshore stations in the Gulf of Mexico. These values are based upon a variety of planktonic and

[1] This study was supported by the Office of Naval Research, Contract No. N00014–68-A-0308–0002.

[2] Present address: Department of Zoology, Miami University, Oxford, Ohio 45056.

benthic invertebrates, as well as fishes, and the study itself represents the beginning step in a long-term effort to establish a biologically meaningful energy budget for the Gulf of Mexico ecosystem.

MATERIALS AND METHODS

All specimens included in the present study were taken during two cruises on the R/V ALAMINOS and one cruise on the R/V ORCA in the spring and summer of 1970 (Table 1). Zooplankton was obtained with a meter tow net, and benthic invertebrates and fishes were captured with a small otter trawl. Immediately following capture, the organisms were sorted, identified, rinsed with fresh water, placed in Saran-wrap or plastic Baggies, and deep frozen. No effort was made to remove the contents of the digestive tracts.

TABLE 1

Source of samples employed in caloric determinations

Code	Cruise and Sta. No.	Date (1970)	Location		Depth of water (m)	Depth of collect. (m)	Sampling gear
			Latitude	Longitude			
	70-A-5						
a	3	3–18	28°11′N	95°25′W	42	10	1-m plankton net
b	16	3–19	28°45′N	94°10′W	26	10	1-m plankton net
c	25	3–20	28°45′N	93°30′W	27	10	1-m plankton net
	70-A-8						
d	29	6–1	23°29.5′N	94°30.5′W	3586	10	1-m plankton net
e	32	6–3	26°39.4′N	94°44.5′W	1372	10	1-m plankton net
f	FG	6–4	27°47.5′N	93°48.5′W	18	10	1-m plankton net
	70-O-1						
g	1	7–19	29°01′N	94°29.3′W	18	18	10′ otter trawl
h	2	7–19	28°18.2′N	94°04′W	55	55	10′ otter trawl
i	6	7–21	28°56.4′N	94°42.3′W	14	14	10′ otter trawl
j	7	7–21	29°50′N	94°42.3′W	14	14	10′ otter trawl
k	8	7–22	29°03.7′N	94°41.5′W	14	14	10′ otter trawl
l	10	7–22	28°57.9′N	94°53.3′W	15	15	10′ otter trawl
m	12	7–23	28°45′N	94°53.5′W	18	18	10′ otter trawl
n	13	7–23	28°55′N	95°03′W	17	17	10′ otter trawl
o	14	7–23	29°08′N	94°53′W	11	11	10′ otter trawl

Prior to combustion the animals were thawed and dried to constant weight at 60° or 80°C. Appropriate conversions were made later, and all values are expressed on the basis of a drying temperature of 80°C. Caloric determinations were carried out with a Phillipson microbomb calorimeter (Phillipson, 1964). Instrument calibration and sample preparation are discussed elsewhere (Wissing and Hasler, 1968). Correction was made for heat input to the fuse wire in the bomb, but not for by-products of combustion such as sulfur and acid, which were assumed to have been negligible. Samples in which the amount of dry material was small or in which the percentage of inorganic matter was high were enriched with measured quantities of benzoic acid to insure complete combustion.

Ashing was carried out at 550°C. In early studies the post-combustion residue was employed for ashing, but later investigation revealed the desirability of ashing an independent sample, since the early values were too low. Where the early values have been retained, they have been adjusted accordingly. In the tables the caloric values are expressed as calories per gram of both dry and ash-free weights.

RESULTS AND DISCUSSION

The caloric determinations are presented in Tables 2, 3, and 4. Since the com-

TABLE 2

Caloric values of planktonic invertebrates and lower chordates from the Gulf of Mexico

Taxonomic identity	Source (code)	Samples: No.	Samples: Avg. dry wt. of individuals (mg)	No. of dets.	Cal/gm dry wt.: Avg.	Cal/gm dry wt.: Range	Cal/gm ash-free wt.: Avg.	Cal/gm ash-free wt.: Range	Ash (% of dry wt.): Avg.	Ash (% of dry wt.): Range
Coelenterata										
Physalia	c	1	97.8	3	3759	3591–3886	4185	3938–4360	13.3	11.9–16.2
siphonophores	c	3	1.8	2	3768	2375–5161	4096	2809–5385	8.5	7.3– 9.8
Ctenophora										
Beroë	b.g	9	1.7	2	3511	3186–3835	3757	3735–3779	9.4	0.2–18.8
Annelida										
alciopid	c	1	4.5	1	3999		4187		4.3	
Mollusca										
Janthina (with shell)	d.e.	4	4.2	2	4031	3683–4379	4862	4276–5450	21.4	18.1–24.8
small squids (undet.)	d.f	11	3.3	5	5408	5010–6252	5559	4960–6285	7.5	3.8–11.2
Arthropoda										
copepods (calanoid)	a	11	0.2	1	6626		6626		<0.1	
stomatopod (larva)	c	1	10.2	1	5390		5434		2.8	
mysids	b	6	0.1	1	7533		7533		<0.1	
isopods	e,f	9	3.4	2	3290	2992–3589	4143	3907–4380	25.4	22.2–28.6
amphipods	a,c	23	0.6	2	3635	3474–3797	4344	4156–4532	20.0	11.8–28.2
decapod larvae (undet.)	a,b,c	16	0.7	3	6816	5923–7670	7010	6566–7588	6.5	0.2–13.1
Lucifer faxoni (ad.)	a,b	53	0.2	2	5552	5187–5916	6130	5943–6316	9.3	9.1– 9.6
sergestid shrimp	e	12	18.4	12	4895	4501–5400	5371	4900–6303	11.8	4.3–19.4
small shrimp (undet.)	d,e	6	2.6	2	4870	3756–5984	5698	4517–6879	17.6	14.7–20.7
small crab (undet.)	f	1	11.8	1	3823		4435		17.9	
Chordata										
salps (undet.)	g	14	1.5	1	3952		5491		34.2	
cyclosalps (colonial)	c	1	22.6	1	5783		6131		8.0	
Average					4813		5052		13.6	

TABLE 3

Caloric values of benthic invertebrates from the Gulf of Mexico

Taxonomic identity	Source (code)	Samples: No.	Samples: Avg. dry wt. of individuals (mg)	Samples: No. of dets.	Cal/gm dry wt.: Avg.	Cal/gm dry wt.: Range	Cal/gm ash-free wt.: Avg.	Cal/gm ash-free wt.: Range	Ash (% of dry wt.): Avg.	Ash (% of dry wt.): Range
Mollusca										
Loligo pealii (juv.)	g.k	20	128.9	10	5473	4952–6188	5700	5288–6187	4.9	0.9– 8.9
Octopus vulgaris (juv.)	i	1	110.8	3	5091	4873–5374	5412	5222–5656	8.7	8.1– 9.3
egg cases (squid)	m	3		3	3368	3167–3550	4233	4048–4502	25.3	18.5–30.5
Arthropoda										
Squilla mantis (juv.)	g	9	5.9	2	4827	4677–4978	5087	4923–5251	7.3	7.3– 7.4
Squilla mantis (ad.)	g,j,l	10	310.9	8	3254	2750–3762	4032	3473–4563	23.8	20.5–26.0
amphipods	n	467	0.3	3	2965	2936–2979	3265	3099–3594	12.0	6.7–21.4
Sicyonia brevirostris	g	2	1,850.4	6	3558	3051–3947	4350	3879–4671	22.9	17.2–26.8
Sicyonia dorsalis	l	2	217.6	6	3503	3276–3643	4201	4039–4354	20.9	18.0–23.5
Crangon sp.	n	3	91.1	3	4143	4015–4254	4894	4675–5023	18.6	16.9–21.1
pagurid crabs (juv.)	o	2	156.2	3	3221	3131–3356	4198	4003–4301	28.6	26.8–32.0
pagurid crabs (ad.)	i	1	3,629.7	3	3088	2854–3286	4167	4090–4280	31.3	28.6–36.1
xanthid crabs (juv.)	n	3	55.1	3	3353	3131–3725	4303	3759–4845	26.9	21.1–31.2
Average					3820		4487		19.3	

TABLE 4

Caloric values of larval and juvenile fishes from the Gulf of Mexico

Taxonomic identity	Source (code)	Samples: No.	Samples: Avg. dry wt. of individuals (mg)	Samples: No. of dets.	Cal/gm dry wt.: Avg.	Cal/gm dry wt.: Range	Cal/gm ash-free wt.: Avg.	Cal/gm ash-free wt.: Range	Ash (% of dry wt.): Avg.	Ash (% of dry wt.): Range
Clupeiformes										
clupeoid larvae	b	45	0.9	2	5508	5486–5530	5725	5676–5776	5.5	4.7– 6.5
Anchoa sp.	j	1	807.8	3	5395	5326–5449	5638	5464–5835	6.7	4.9– 9.1
Myctophiformes										
Synodus foetens	h,j	2	584.9	6	5120	4639–5557	5916	5252–6194	18.9	15.2–25.4
Anguilliformes										
leptocephalus larvae	b,e,g	6	25.7	10	5303	4661–5972	5680	4964–6391	9.1	1.5–20.7
Beloniformes										
Strongylura sp.	k	2	68.7	5	5023	4722–5612	5507	5266–5970	12.0	8.6–14.7
Perciformes										
perciform larvae (undet.)	d,f,h	38	2.2	5	5680	4047–6846	6105	4517–6996	10.1	3.1–16.0
serranid	j	1	1,137.3	3	4758	4680–4856	5541	5412–5703	18.0	16.1–18.9
caranigids	j,k	2	1,028.7	6	4670	4478–4843	5172	4900–5706	12.8	6.9–21.3
Cynoscion sp.	j,k	2	428.8	7	4906	4683–5055	5508	5281–5691	15.1	10.7–18.4
Prionotus sp.	g	1	715.7	3	4261	4065–4406	5074	4887–5248	20.7	18.2–24.8
Stenotomus caprinus	j	1	833.8	3	4759	4526–5063	5716	5351–5974	20.9	16.6–26.6
Pleuronectiformes										
bothids	h,j	3	361.8	9	4926	4602–5201	5331	4938–5573	10.1	6.6–17.3
Tetraodontiformes										
Lagocephalus laevigatus	j	1	194.4	3	4874	4548–5154	5525	5392–5662	15.3	9.4–24.4
Average					5014		5572		13.5	

bustion technique was found to give highly reproducible results with benzoic acid and homogeneous organic material, the relatively high sample variability evident in the tables is assumed to reflect sample heterogeneity resulting from variation in gut contents, size of individual organisms, and species composition within a general taxonomic category. Such data, of course, reflect the type of nutritional variability encountered by the browsers and predators which consume these organisms. Considering the fact that in most instances only a small number of determinations was made and the fact that intersample variability was high, the data must be interpreted with some caution. Nevertheless, certain data trends are evident and deserve mention.

The overall average caloric value for the zooplankton groups examined is 5052 cal/gm ash-free weight with an average ash content of 13.6%. These values compare closely with those given by Ostapenya (1966) for unsorted zooplankton samples from the Gulf of Mexico (5001 cal/gm and 13.1%) and for the Cuban Shelf (5144 cal/gm and 14.0%). Among the zooplankton groups, the lower phyla average between 3750 and 4200 cal/gm, the mollusks between 4850 and 5600 cal/gm, whereas the crustaceans, with a few exceptions, range between 5300 and 7550 cal/gm. Viewed from an ecological standpoint certain of the organisms examined maintain a low body density (and hence are able to float) by means of gas bubbles. These forms, including *Physalia*, siphonophores, and the snail *Janthina*, tend to have low caloric values. Another group consists of rather active swimmers (*Beroë*, the alciopid annelid, isopods, amphipods, and small crab). These also show low caloric values. The remainder of the planktonic invertebrates are relatively small and inactive, and their uniformly high caloric values suggest high lipid contents which would provide bouyancy in the warm Gulf waters.

The benthic invertebrates were found to range between 3250 and 5700 cal/gm. Those which are more strictly bottom-dwelling tended to range below 5000 cal/gm, whereas the *Loligo*, *Octopus*, and juvenile *Squilla* which must spend at least part of their time in the water column were all above 5000 cal/gm. The average ash content of the benthic invertebrates was considerably higher than that of the planktonic forms, but variability was noted in both cases.

As a group the fishes were quite uniform, individual species ranging between 5050 and 6100 cal/gm (with an overall average of 5572). Larval forms gave especially high values. The ash content was lowest for the larval forms, but otherwise quite uniform. On the average, the ash content was similar to that of the planktonic invertebrates.

In overview, this brief survey of caloric values and ash contents of marine animals from the Gulf of Mexico suggests a number of biologically interesting trends. A tentative case can be made that invertebrates which are benthic, which employ gas bubbles for floating, or which are small active swimmers have low caloric values, whereas the more passive invertebrates of the water column have relatively high caloric values, in some cases exceeding 7500 cal/gm. Among the fishes the larval forms tend to have higher caloric values than the adults, although this comparison may be confounded, to some extent, by the fact that some of the species possess swim bladders while others do not. Ash contents tend to be highest among the benthic forms, but the correlation is not exact.

At very least the present study opens the door to further broad investigation in which caloric and ash contents are related to bouyancy and life style. In continuation, these factors should be investigated in relation to lipid content and body density.

ACKNOWLEDGMENTS

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EFFECT OF SALINITY ON ACUTE TOXICITY OF MERCURY, COPPER, AND CHROMIUM FOR *RANGIA CUNEATA* (PELECYPODA, MACTRIDAE)

Karen R. Olson and Richard C. Harrel

Department of Biology, Lamar University, Beaumont, Texas 77710

ABSTRACT

The 48, 72, and 96 hour median tolerance limits (TL_m) for mercury, copper, and chromium were determined for *Rangia cuneata* at salinities of less than 1 ppt, 5.5 ppt, and 22 ppt. All of the ions were more toxic in freshwater than in more saline waters. Copper and chromium were most toxic; less than 1 ppm was required for a 48 hour TL_m. At 22 ppt salinity all salts required more than 10 ppm for a 48 hour TL_m.

INTRODUCTION

Rangia cuneata, a brackish water clam, is found in large numbers in the lower Neches River of southeast Texas. The river receives many industrial wastes, and cities along the river are interested in attracting other industries, which might also add waste effluents to the river. Presently very little is known about the effects of the wastes on *Rangia*.

Rangia is an important member of the estuarine fauna (Hopkins and Andrews, 1970). Being a filter feeder, it converts detritus into protoplasm and serves as a source of food for several fishes, crabs, and shrimp (Tarver, 1970; Fairbanks, 1963). This clam is presently canned for food in part of its distribution range and has potential value as food throughout the range (Wolfe and Petteway, 1968). The shell is of commercial value in Louisiana (Tarver, 1970; Odum, 1967). Hopkins (1970) suggested that the Neches River population could be profitably harvested. *Rangia* is suitable as an assay animal as it is easily collected and very easy to handle in the laboratory.

The median tolerance limits of *Rangia* for three metal ions at various salinities were investigated during this study. The ions were copper (copper sulfate), mercury (mercuric chloride), and chromium (potassium dichromate). All are found in the wastes of local industrial processes and have been used in toxicity studies for other animals.

MATERIALS AND METHODS

Three salinity concentrations were selected. The lowest was less than 1 ppt, which represents the condition of the river for most of the year. An intermediate salinity of 5.5 ppt, and a high concentration of 22 ppt were also investigated. These salinities approximate the normal range

from which living *Rangia* have been collected in the Neches River. The room temperature was approximately 24°C. Oxygen tension was not monitored, but the shallow depth of the water would make it improbable for the water to have been less than saturated for the conditions at any time.

The procedures used to determine the TL_m were essentially those listed in *Standard Methods.* (American Public Health Assoc., 1965).

Clams were taken from the river at frequent intervals and held in the laboratory in 12 to 18 liters of salinity-adjusted water in polyethylene containers. The clams were initially held at a salinity of either less than 1 ppt or at 5.5 ppt. Animals to be used in the high salinity tests were transferred to higher salinities after a day or more at low salinity. Water in the holding pans was circulated and salinity was adjusted with "Instant Ocean." Clams were not used if they had been in the laboratory for more than a month, and most were used within two weeks.

After the approximate range of lethal concentrations had been determined in preliminary tests, full scale tests were run. A series of pans, each containing six liters of test solution and 15 clams, was prepared. There were two pans (30 clams) for each concentration, and each concentration was double the preceding one. If more points were required to establish results, only one pan was used for each dilution. Five dilutions were usually adequate to determine the tolerance limits sought.

Test containers were checked at the same time daily and clams found dead between scheduled inspections were removed and counted with the next time interval. Each clam was inspected each day. Test solutions were normally not changed during the four day experiment. However, in some cases fungi invaded the containers and the solutions were changed after the second day.

The TL_m was determined in the manner described in *Standard Methods* . . . (American Public Health Assoc, 1965). Salt concentration was plotted on the logarithmic scale and percent survival on the arithmetic scale of semi-logarithmic graph paper. The concentration corresponding to the point that the line crossed the 50 percent survival point was designated the TL_m concentration for the salinity and time.

RESULTS AND DISCUSSION

Each of the metal salts was toxic to *Rangia* at all salinities in some concentration. Table 1 presents all the median tolerance limits determined. The mercury TL_m was lowest in less than 1 ppt salinity (Fig. 1). *Rangia* was most resistant to mercury when salinity was 5.5 ppt. Copper, like mercury, was least toxic when

TABLE 1

Salinity effects on median tolerance limits for mercury, copper, and chromium

Salinity (ppt)	Ion Conc. for TL_m (ppm)		
	48 hrs.	72 hrs.	96 hrs.
	MERCURY		
Less than 1	6.3	5.5	5.1
5.5	40.0	20.0	10.0
22	17.0	9.5	8.7
	COPPER		
Less than 1	0.78	0.25	0.21
5.5	16.0	11.7	8.0
22	14.7	10.0	7.4
	CHROMIUM		
Less than 1	0.96	0.32	0.21
5.5	66.0	32.0	14.0
22	86.0	73.0	35.0

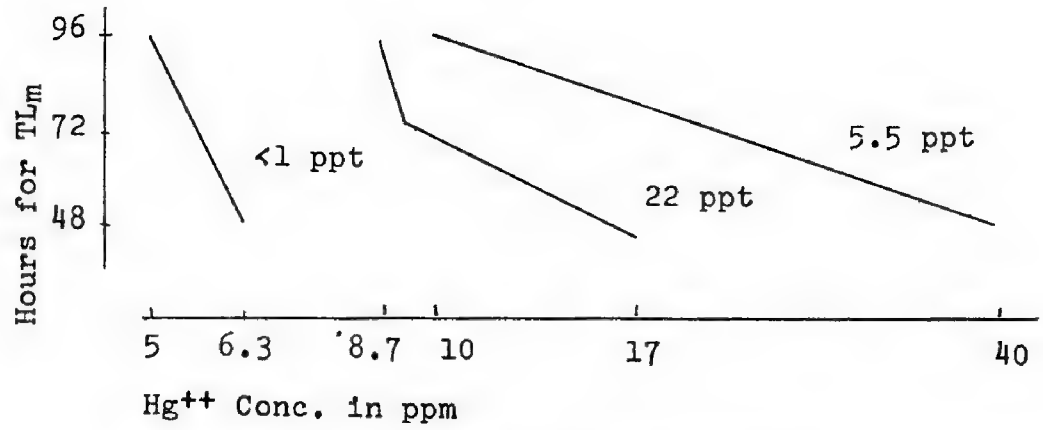

FIG. 1. Effect of salinity upon toxicity of mercury ions.

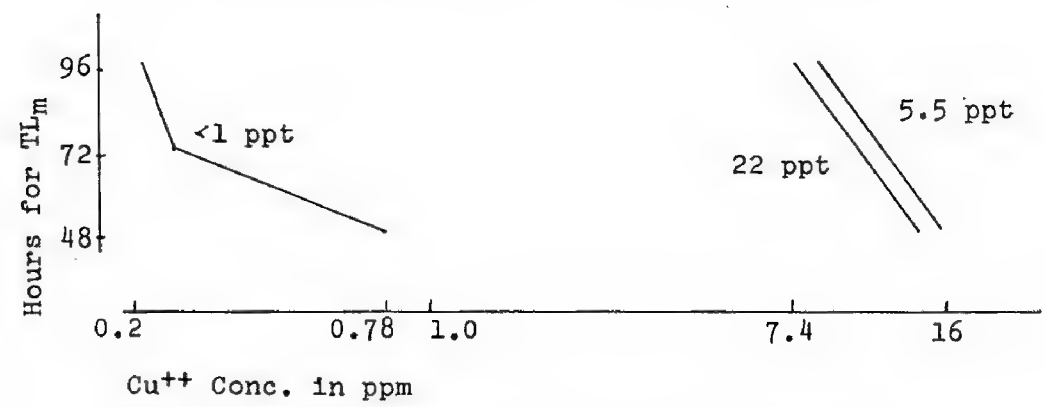

FIG. 2. Effect of salinity upon toxicity of copper ions.

salinity was 5.5 ppt, but toxicity for this concentration is almost the same as that at 22 ppt (Fig. 2). Chromium was also most toxic at less than 1 ppt (Fig. 2). Chromium was also most toxic at less than 1 ppt salinity (Fig. 3). However, chromium was least toxic at 22 ppt salinity rather than at the intermediate level.

In freshwater (Fig. 4), copper was the most toxic ion, with chromium almost as toxic. A concentration of less than 1 ppm was lethal to half of the test animals within 48 hours for both ions. Mercury was much less toxic, for 6 ppm were required to establish a 48 hour TL_m. At 5.5 ppt salinity (Fig. 5) *Rangia* was most sensitive to copper with a 48 hour TL_m of 16 ppm. Chromium was the least toxic at the intermediate salinity requiring 66 ppm to establish a 48 hour TL_m. With 22 ppt salinity (Fig. 6) the 48 hour TL_m for both copper and mercury were approximately 15 ppm. Chromium was much less toxic at the high salinity with an 86 ppm concentration for a 48 hour TL_m.

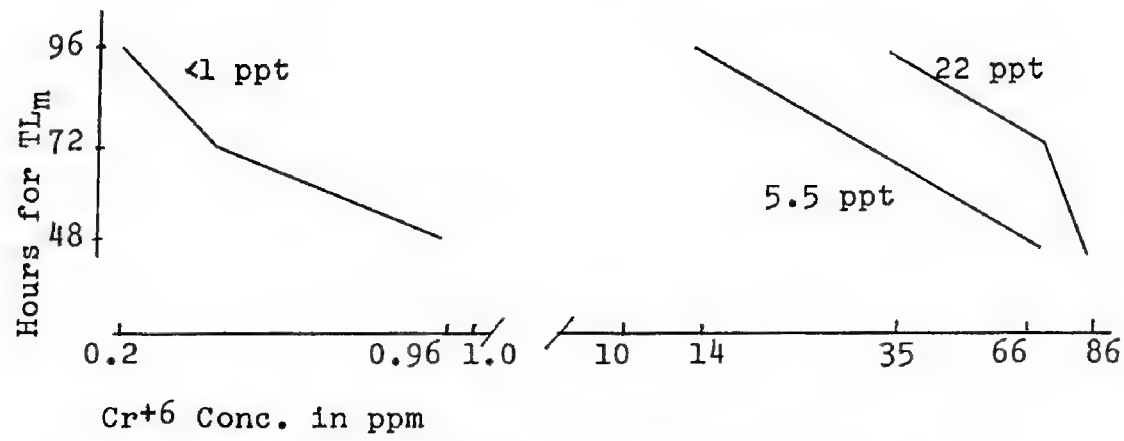

FIG. 3. Effect of salinity upon toxicity of chromium ions.

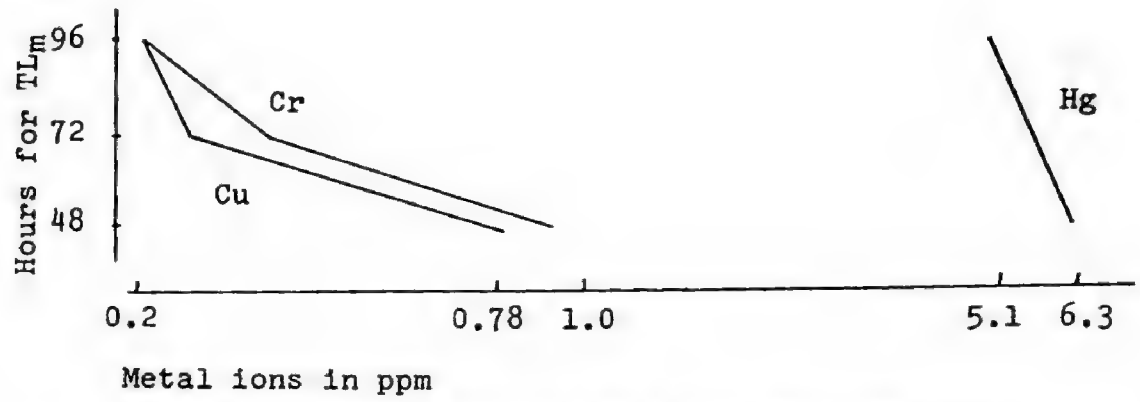

FIG. 4. Comparison of toxicity with salinity less than 1 ppt.

The relatively low concentration, less than 1 ppm, required for acute toxicity of copper and chromium in fresh water suggest possible danger to *Rangia*. The higher concentration, above 7 ppm, of any of the ions to produce even a 96 hour TL_m with increased salinity might appear to be higher than would be reached under most conditions in flowing water. However these are acute, not chronic, toxicities and much lower concentrations may be toxic over an extended time. As is the case with many rivers with upstream dams, the water flow in the lower Neches virtually ceases in the summer resulting in a "holding pond" in which the effluent concentration builds. This suggests the desirability of long term toxicity studies to determine chronic toxicity limits. The effect of temperature on both acute and chronic toxicity might also provide useful information.

This study investigated the acute toxicity on *Rangia cuneata* of three metal salts as it was affected by salinity. In other studies both mercury and copper were often toxic to invertebrates in a range of 0.01 ppm to 3 ppm, with mercury

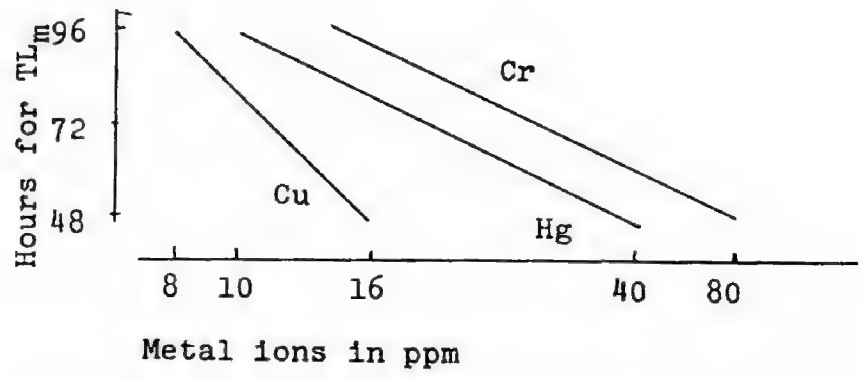

FIG. 5. Comparison of toxicity with salinity of 5.5 ppt.

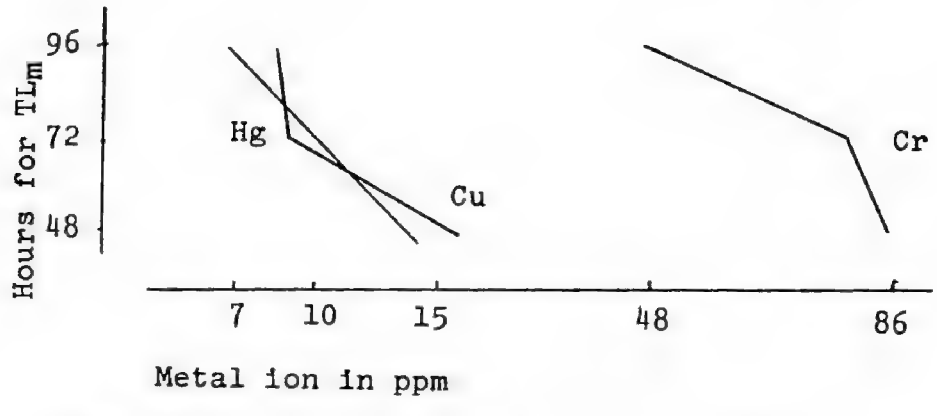

FIG. 6. Comparison of toxicity with salinity of 22 ppt.

being more toxic. Lethal limits for fish varied much more (McKee and Wolf, 1963; Ellis, 1937). *Rangia* was less sensitive to mercury in fresh water than most invertebrates reported. It was equally sensitive to copper as most other invertebrates in freshwater (McKee and Wolf, 1963; Reish, 1964). In more saline water it appeared to be more copper tolerant than either the mussel, *Mytilus edulis*, which shares its salinity range, or oysters which generally inhabit a more saline environment (Wilber, 1969). Chromium was usually much less toxic to animals than either of the other two ions (McKee and Wolf, 1963), but *Rangia* is very sensitive to it in fresh water. Studies need to be made with other organisms so that optimum effluent limits may be set.

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BENTHIC MARINE ALGAL ECOLOGY IN THE PORT ARANSAS, TEXAS AREA

Peter Edwards[1] and Donald F. Kapraun[2]

Department of Botany, The University of Texas, Austin, Texas 78712

ABSTRACT

The benthic marine algal flora in the vicinity of the University of Texas Marine Science Institute at Port Aransas was studied at 26 monthly intervals. Eighty-nine species from 52 genera, were collected during the study. The flora was considered in terms of the spatial and seasonal distribution of the species, the former being divided into horizontal and vertical components. The horizontal distribution was further divided into small scale or local and large scale or geographical distribution. Correlations were sought between the observed distribution of each local species in the area and various environmental factors in an attempt to determine the causal factors of the distribution of benthic marine algae. The major characteristic of the flora was its dynamism. The regular seasonal changes in the vegetation brought about largely by the pronounced annual temperature range of 17°C, contrasted with the irregular changes in the local distribution between the two years, caused by erratic rainfall distribution with concomitant salinity variations and the occurrence of a hurricane.

INTRODUCTION

The benthic marine algal flora of Texas in the Gulf of Mexico is among the least studied on the eastern seaboard of the United States. The shoreline is composed predominantly of unconsolidated sediments which form a barrier island, behind which are shallow bays containing oyster reefs and grass flats which support a varied flora. Tidal inlets across the barrier island have been stabilized to form ship passes by the construction of pairs of stone jetties, which provide an ideal habitat for the growth of benthis algae. Other areas on the eastern seaboard of the United States with similar habitats, e.g., Chesapeake Bay and the Tampa, Florida area, which were formerly considered to be barren, presumably because of an absence of a rocky shore, have since been shown to possess a well developed flora (Dawes, 1967; Phillips, 1960b; Zaneveld & Barnes, 1965).

Earlier studies in Texas were largely compilations of species (Taylor, 1935, 1936, 1941; Humm & Hildebrand, 1962). Taylor (1941, 1955) considered that the flora of the northwestern Gulf of Mexico was probably an impoverished tropical Caribbean flora without a marked temperate element, but Conover

[1] Present address: Department of Botany, Nelson Biological Laboratories, Rutgers University, New Brunswick, New Jersey 08903.

[2] Present address: Department of Biology, The University of North Carolina at Wilmington, Wilmington, North Carolina 28401.

(1964) in his seasonal study of benthic communities along a 180 km strip of the Texas coast demonstrated clearly that although the largest part of the flora is of tropical affinity, a distinctive cool temperate element develops in the area during the winter and early spring.

The present contribution was an intensive seasonal study of a relatively small area in the vicinity of the University of Texas Marine Science Institute at Port Aransas. The flora was considered in terms of the spatial and seasonal distribution of the species. Correlations were sought between environmental factors and the observed distribution of species in an attempt to unravel the causal factors in the distribution of benthic marine algae. The spatial distribution was considered in terms of its horizontal and vertical components; the former was divided further into small scale or local distribution and large scale or geographical distribution and from the latter the floristic affinity of the flora was determined.

MATERIALS AND METHODS

Description of the area

The area in which the field studies were conducted lies to the northeast of Corpus Christi, Texas, in the northwest corner of the Gulf of Mexico at approximately 28°N 97°W (Fig. 1). The coast of Texas consists of a barrier island which fronts a coastal lagoon, but in the study area the lagoon has been broken up into a series of relatively shallow bays. The outer shoreline of the barrier island comprises a beach of fine, unconsolidated sand which provides an inhospitable environment for benthic marine algae due to wave action and the absence of solid substrata. The bays behind the barrier island are connected to the open sea by a tidal inlet at Port Aransas about 0.5 km wide, which has been stabilized by the construction of a pair of stone jetties about 2.5 km long which extend out into the sea. The jetties are roughly triangular in cross-section, and have an upper surface composed of large granitic quarry blocks weighing several tons each. The quarry blocks have been placed together loosely and thus large cracks and cavities exist which provide shelter. The jetties afford an area of artificially rocky coast on a shore otherwise inhospitable for algae, and they are densely covered by algae.

Redfish and Aransas Bays, situated behind the barrier island, have largely unconsolidated sandy and muddy bottoms which are unsuitable for benthic algal growth. The shallow regions of the bays, however, are often colonized. by extensive beds of seagrasses which stabilize the sediments so that algae may become established. Natural algal substrata in the bays are provided by the seagrasses themselves and by shells, and these are augmented by artificial substrata such as seawalls, bridge supports and pier posts.

Stations

Benthic marine algae were collected on a monthly basis over a period of 26 months from June 1967 to July 1969 at the following six localities, which were selected to include a range of habitats (Fig. 1).

Aransas Bay is a relatively calm water bay which had large salinity variations during the study. The habitats sampled were subjected to more wave action than those in Redfish Bay, since waves washed against solid, man-made substrata at the edge of the bay. Algae were sampled from four localities in the bay: Station 1, a beach 1.5 km north of Fulton Harbor. The site

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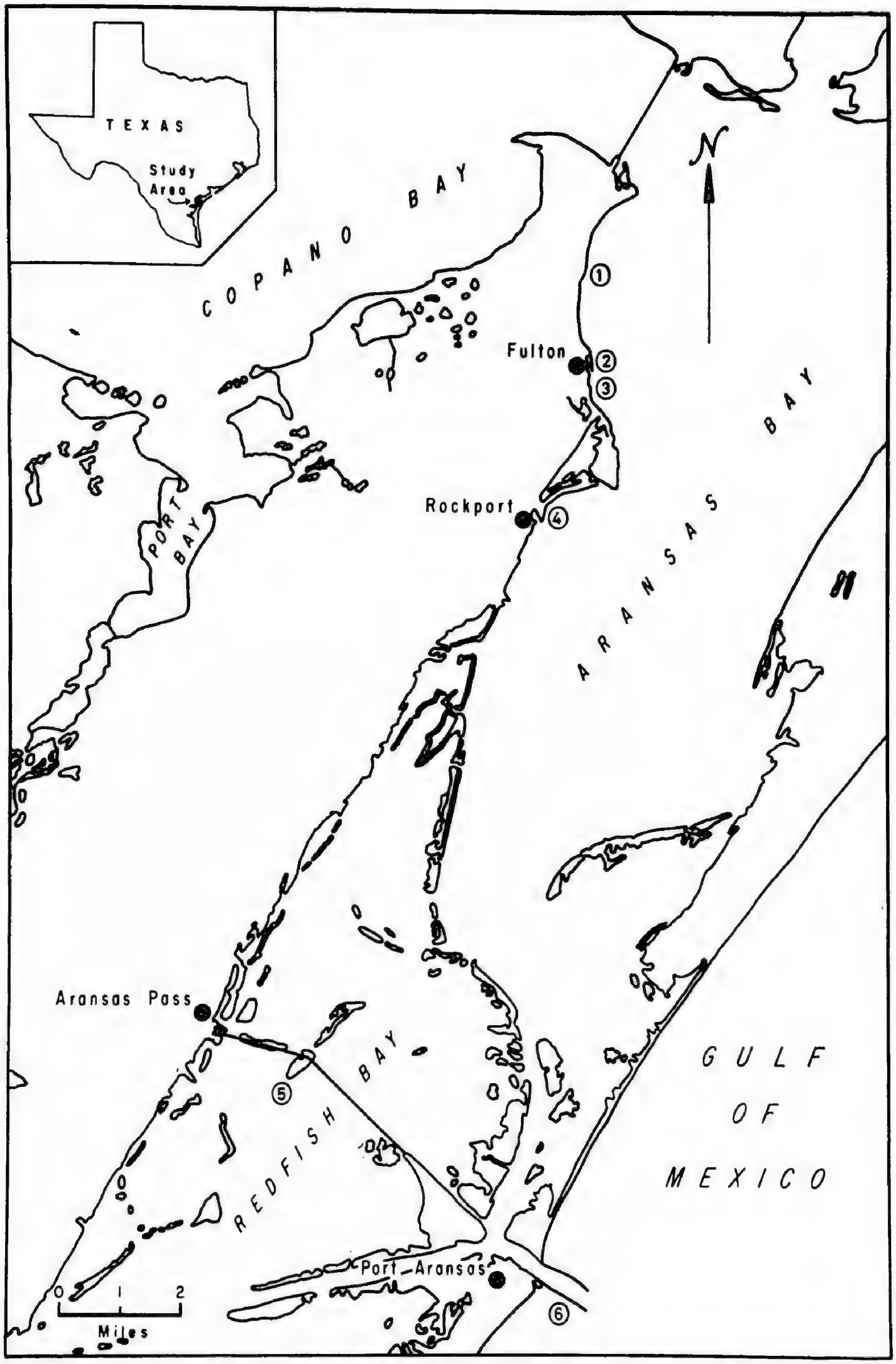
FIG. 1. Map of the study area. The numbers refer to stations at which monthly collections of algae were made. Station 1, Fulton beach; Stations 2 and 3, Fulton Harbor; Station 4, Rockport; Station 5, Redfish Bay; Station 6, the southwest jetty, Port Aransas. Modified from U.S. C. & G.S. Map No. 1285.


TEXAS
Study Area
COPANO BAY
Fulton
Rockport
PORT BAY
ARANSAS BAY
N
Aransas Pass
REDFISH BAY
Port Aransas
GULF OF MEXICO
0 1 2
Miles
①
②
③
④
⑤
⑥

consisted of a gently sloping beach with a soft unstable substratum of sand and shell. Algae were collected on wooden pier supports, on oyster shells, and on concrete and brick rubble at the edge of the bay. Station 2, the concrete base of the fishing pier and the outer side of the concrete harbor wall, Fulton. Station 3, a beach just to the south of the harbor, similar to Station 1 but without a pier. The data from the above two sites has been considered collectively under "Fulton" in Table 1. Station 4, algae were collected on a concrete breakwater and from shells at the edge of the bay at Rockport. This site was subjected to smaller salinity variations than the preceding ones in Aransas Bay.

Redfish Bay is a relatively shallow, calm-water bay with little wave action. Salinity variations were probably less than those in Aransas Bay since the bay is situated closer to the sea than the latter bay, Station 5, algae were collected on grass flats and on an oyster reef. The station was established in June 1968 in the middle of the study.

Algae were collected in two habitats on the southwest jetty, Port Aransas, Station 6: The first (a) was along the entire jetty which was composed largely of granite. The jetty was subject to wave action which increased with distance from the shore. The salinity variations were less than those of the bays. The jetty was the only habitat where the water was sufficiently deep to enable algae to occupy a potentially large vertical range. The second (b) consisted of pools by the beach at the side of the jetty. The beach side of the southwest jetty was flanked by a flat expanse of mud and silty sand. Water was forced through fissures in the jetty from the channel and formed pools up to 25 cm deep. Since the standing water was shallow, it reflected the more extreme air temperatures and was also susceptible to more extreme salinity changes than the sea due to dilution by rain or concentration by evaporation.

The sampling in the latter part of the study was more thorough than that in the former part as experience was gained in the area. The use of cultures was resorted to frequently in the latter part to collect and identify smaller algae, particularly with *Streblonema* and *Acrochaetium* species. *Asterocytis ramosa* was never observed in the field but developed as a contaminant in a culture of a larger alga from Redfish Bay. Zaneveld & Barnes (1965) similarly used cultures in their study of the algae present in Chesapeake Bay.

Specimens collected during the study have been deposited in the herbaria of the University of Texas at Austin and in those of the authors.

RESULTS

The results are presented in Table 1. The local and seasonal distribution of the flora are given, and the reproductive state of each species has been included whenever possible.

Environmental Factors

1. Temperature

A large seasonal variation in the surface water temperature took place in the study area. The minimum average monthly temperature in January was 12.7°C and the maximum average monthly temperature in July was 30°C for Port Aransas (U.S. Department of Commerce, 1965) giving a seasonal range of 17.3°C (Fig. 2). The water temperatures of Aransas and Redfish Bays follow those of the air more closely and thus have an even wider annual range.

2. Light Intensity

Pronounced seasonal fluctuations in light intensity took place in the area. Brownsville, located 240 km southwest, had an average monthly maximum in

TABLE 1 (Part 1)

Species	Locality	1967 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	1968 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	1969 Mar	Apr	May	June	July
Ulothrix flacca	Fulton					—																	x				
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—									x	x				
	Port Aransas					—																					
Ento-cladia viridis	Fulton	x				—																	x	x	x		
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—									x	x				
	Port Aransas	x	x			—																					
Ulvella lens	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—								x						x
	Port Aransas					—																					
Entero-morpha clath-rata	Fulton					—		x	x	x	x	x			x	x		x	x	x	x	x	x	x	x	x	x
	Rockport					—	x	x	x	x		x			x	x	x		x	x	x		x	x	x	x	x
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—										x	x		x	
	Port Aransas	x	x	x	x	x	x	x	x	x	x	x	x		x	x		x	x	x				x	x	x	
Entero-morpha flexuosa	Fulton					—			x	x	x	x						x			x		x	x			
	Rockport			x		—															x	x					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—									x						
	Port Aransas	x	x			—	x		x	x	x	x	x								x		x	x	x		
Entero-morpha linguulata	Fulton					—		x	x		x	x									x	x	x	x			x
	Rockport			x		—	x	x			x			x													
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—								x						
	Port Aransas	x	x	x		x			x	x	x		x					x			x		x	x		x	x
Entero-morpha proli-fera	Fulton					—															x						
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—															
	Port Aransas									x																	
Entero-morpha ramu-losa	Fulton					—						x															
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—															
	Port Aransas		x				x	x	x	x	x		x					x			x		x				

TABLE 1 (Part 1)

Species	Locality	1967 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	1968 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	1969 Mar	Apr	May	June	July
Entero-morpha salina	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas																						x				
Ulva fasciata	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas		x		x		x	x	x	x	x		x	x		x	x	x	x	x	x	x	x	x	x	x	x
Ulva lactuca	Fulton					—				x	x	x									x	x		x	x	x	x
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas	x	x			—		x	x	x	x	x	x			x					x	x	x				x
Chaeto-morpha linum	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—		x	x		x								x	x
	Port Aransas	x	x	x		—						x	x	x	x	x	x	x	x	x	x	x		x	x	x	x
Cladophora albida	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—		x	x	x	x										x	x	x	x	x		
Cladophora dalmatica	Fulton					—	x	x	x	x		x		x	x	x			x	x	x	x	x	x	x	x	x
	Rockport					—						x		x	x	x		x	x		x		x	x	x	x	x
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas	x			—									x													
Cladophora delicatula	Fulton					—									x											x	
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—													x	x
	Port Aransas		x			—										x											
Cladophora ruchingeri	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—																		x			

Clado-	Fulton		x	x		—				x	x	x							x	x		x	x	x	x	x	x	x	x
phora	Rockport	x	x	x		—													x	x			x		x		x
vaga-	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																	x
bunda	Port Aransas	x	x	x	x	—	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Derbesia	Fulton					—																								
vaucher-	Rockport					—																								
iaeformis	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																	
	Port Aransas					—																						s	x	
Bryopsis	Fulton					—																								
hypnoides	Rockport					—																								
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																	
	Port Aransas	x	x	x		—										x	x	x									x	x	x
Bryopsis	Fulton					—																								
plumosa	Rockport					—																								
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																	
	Port Aransas					—																							x	x
Acetabu-	Fulton		x	x		—						x	x										x		x	x			x
laria	Rockport					—																								
crenulata	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x									x	x			
	Port Aransas					—																								
Ecto-	Fulton					—		p	x,p	p	x,p								x,p	p		x,p	x,p	p	x				
carpus	Rockport					—		p	p	p	x,p	x,p								p		p	p	p					
silicu-	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																	
losus	Port Aransas					—																								
Giffordia	Fulton					—																								
indica	Rockport					—																								
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																	
	Port Aransas					—						p	p	p	p				p	p		p		p				p	
Giffordia	Fulton	p	p	p		—	p	p				p	p				p	p	p	p										
mitchel-	Rockport	p	p			—	p									p		p	p						p					
liae	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—											p						
	Port Aransas		p			—	p,u	p,u	p	p	p	p	p							p		p					p			

TABLE 1 (Part 2)

Species	Locality	1967 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	1968 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	1969 Mar	Apr	May	June	July
Giffordia rallsiae	Fulton					—													p		p	p	p	p	p		p
	Rockport					—														p	p	p	p	p		p	p	p
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	p												p		
	Port Aransas					—								p		p	p			p				p	p	p	p	p
Streblonema oligosporum	Fulton					—																	p	p	p			
	Rockport					—																						
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—															
	Port Aransas					—																p	p					
Streblonema sp.	Fulton					—																						
	Rockport					—																						
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—															
	Port Aransas					—																		p		p		
Dictyota dichotoma	Fulton					—																						
	Rockport	t	x,f			—																						
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—						x						x	x	x	
	Port Aransas		x,t	x		—								x	x	x,t	t	x,t	x,t	t	x				f,t	t	x,t	
Padina vickersiae	Fulton					—																						
	Rockport	x	x	x,f		—																						
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—															
	Port Aransas	t	x,t	x,m f,t		—		x	x,t					x,m	x,t	x,f	x	x,m	x,t	x	x	x	x	x	t	x	x	x,t
Cladosiphon occidentalis	Fulton					—																						
	Rockport					—																						
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—										p,u					
	Port Aransas					—																						
Stictyosiphon subsimplex	Fulton					—																	x					
	Rockport					—																x						
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—									x	x	x				
	Port Aransas					—																						
Myriotrichia subcorymbosa	Fulton					—																		p				
	Rockport					—																						
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	p										p	p	p	p	
	Port Aransas					—																						

Peta-lonia fascia	Fulton					—																										
	Rockport					—																										
	Redfish Bay	—	—	—	—	—	—	—		—	—	—	—	—																		
	Port Aransas					—		x		p	p	p	p												p	p	p	p				
Gonio-trichum alsidii	Fulton			x		—																										
	Rockport		x	x		—																										
	Redfish Bay	—	—	—	—	—	—	—		—	—	—	—	—																		
	Port Aransas		x	x		—		x							x	x	x	x	x											x	x
Erythro-cladia subin-tegra	Fulton			x		—																										
	Rockport				x	—											x															
	Redfish Bay	—	—	—	—	—	—	—		—	—	—	—	—																		
	Port Aransas	x	x			—		x		x	x	x'	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x		
Erythro-trichia carnea	Fulton					—																										
	Rockport			x		—																										
	Redfish Bay	—	—	—	—	—	—	—		—	—	—	—	—																	x	x
	Port Aransas		x			—	x	x		x		x	x	x	x	x	x	x	x	x				x					x	x	x	
Bangia fusco-purpurea	Fulton					—																										
	Rockport					—																										
	Redfish Bay	—	—	—	—	—	—	—		—	—	—	—	—																		
	Port Aransas		a,b			—	a,b	a,b		a,b	a,b		a,b	a,b				a,b	a,b	a,b	a,b	a,b	a	a,b	a,b	a	a,b	a,b	a			
Porphyra leuco-sticta	Fulton					—																										
	Rockport					—																										
	Redfish Bay	—	—	—	—	—	—	—		—	—	—	—	—																		
	Port Aransas					—				a,b	a,b	a,b	a,b											a,b	a,b	a,b	a,b					
Acro-chaetium trifilum	Fulton			x		—																										
	Rockport			x		—																										
	Redfish Bay	—	—	—	—	—	—	—		—	—	—	—	—																		
	Port Aransas	x	x	x		—	x	x		x		x		x	x	x	x	x	x	x	x			x		x	x	x	x	x		
Acro-chaetium flexuosum	Fulton				x	—	x	x		x	x		x	x					x		x	x	x	x	x	x	x					
	Rockport					—					x							x		x			x	x	x	x						
	Redfish Bay	—	—	—	—	—	—	—		—	—	—	—	—																		
	Port Aransas					—												x														x

TABLE 1 (Part 2)

Species	Locality	1967 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	1968 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	1969 Mar	Apr	May	June	July
Acro-chaetium hoytii	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—									x											x	x
Acro-chaetium seriatum	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—									x											x	
Acro-chaetium virga-tulum	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	--	—	—	—	—	x	x								x	x	x	x	x
	Port Aransas					—																					
Gelidium crinale	Fulton		m,t	x	x	—	t	x	x	x	t	f	x,t	x				x	x	x	x	x,t	f	x	x	x	x
	Rockport	x	x	x		—	x	x	x	x,m	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas		x,t	x,m	m,t	—	x,m f,t	t	t	x,t	x,m t	t	x,m t	x,t	x	x,t	x,f t	x,f t	t	x,t	t	x,t	x,t	x,t	x,f	t	x,m t
Ptero-cladia bart-lettii	Fulton					—																					
	Rockport		m,t	m		—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—																					
Ptero-cladia capillacea	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—		x,f						f,t	x,t		x,f t	f,t	t	t	t	x	x	f	x	x	x
Hetero-derma lejolisii	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	c	c				c		c	c	x	c	c	c	c
	Port Aransas					—																					
Derma-tolithon pustu-latum	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	c	c						c	c	c	c	c	c	c
	Port Aransas	c	c	c		—	c	c	c	c	c		c	c	c		c	c	c	c	c	c	c	c	c	c	c

Coral-lina cubensis	Fulton					—																							
	Rockport					—																							
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—										x			x	x		
	Port Aransas		x			—																				x	x		
Coral-lina subulata	Fulton					—																							
	Rockport					—																							
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																
	Port Aransas		x,c	x		—	x	x	x	x,c	x	x	x,c	x	x	x	x	x	c	x	x,c	x	x	c	c	x,c	x,c		
Grate-loupia filicina	Fulton					—				x													x				x		
	Rockport					—													x	x			x		t				
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																
	Rockport		x,f t			—	x		x,t	x,t	x,t	t	x,t	x,f	x	x,f t	x,f t	f,t	x,t	x,t	x,t	t	x	f,t	x,t	x,f			
Agard-hiella baileyi	Fulton					—																							
	Rockport					—																							
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—									x	x	x,f		f			
	Port Aransas					—																		t					
Agard-hiella tenera	Fulton					—																							
	Rockport					—																							
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																
	Port Aransas	f,t	m,f	f		—	x,f	x,t	x	x	x,t		x,t	x	x,f	x,f t	x,m f	f,t	f,t	x,f	f				x,t	x,f t	x,f t		
Hypnea cornuta	Fulton			x		—																							
	Rockport	x	x	x		—																							
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—											x	x		x		
	Port Aransas		x			—								x,t	x,t	x	x,t	x,t					x	x	t	x			
Hypnea musci-formis	Fulton		x	x		—																							
	Rockport	x,m	x	x		—																							
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	x		x	x	x	x	x	x	x	x	x	x	x	x		
	Port Aransas	m,t	x,m f,t	x,f		—	f,t	t	x	x	x	t	m,t	x,t	x,f t	s,t	x,f t	f,t	m,f	x	x,t	x	x	f,t	f,t	x,t	x		
Graci-laria debilis	Fulton					—																							
	Rockport					—																							
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x		x	x	x		x		x	x	x		
	Port Aransas					—																							

TABLE 1 (Part 3)

Species	Locality	1967 June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	1968 June	July	Aug	Sep	Oct	Nov	Dec	1969 Jan	Feb	Mar	Apr	May	June	July
Graci-	Fulton	x,t	x,t	x,f t	x,f t	—	x	x,t	x	x,t	x	x		x		x				x	x	x,f t	x,f	f,t	x,f t	t	x,m t
laria	Rockport	x,f t	x,f t	x,f t	x,f	—	x	x	x	x	x	x,f	x,f t	x,t	x	x,f	x	t	x		x,t	f,t	f,t	f,t	f	x,f t		
foliifera	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	x,f t	t			x,t	x	m,t	t	x,f	x,f t	f	f,t	f,t	x,f
	Port Aransas	x	x			—			t	x	x			x,t	x,m t	x,f t	f,t	x,f t		x	x,f			m,f t	f,t	f,t	f,t
Graci-	Fulton					—																					
laria	Rockport					—																					
verru-	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x			x	x					x	x	x
cosa	Port Aransas					—																					
Rhody-	Fulton					—																					
menia	Rockport					—																					
pseudo-	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
palmata	Port Aransas	f	f,t	x,f t		—	x,m	t	x	f	x,m f,t	f	x,t	x,t	x	x	x	x,t	t	x,f	f,t	f,t	f,t	f,t	x,f	f	f,t
Lomen-	Fulton					—																					
taria	Rockport					—																					
bailyana	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—								x													x
Champia	Fulton					—																					
parvula	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—									x	x	x	x		x
	Port Aransas					—																					
Calli-	Fulton					—																					
thamnion	Rockport					—																					
byssoides	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas	t		t		—	m,t				x,m		t			t	x								x,m t	x,m t	f
Griffithsia	Fulton					—																					
tenuis	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—									t					
	Port Aransas					—																					

Spermothamnion sp.	Fulton					—																											
	Rockport					—																											
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																				
	Port Aransas	x	x	x		—	x		x					x	x									x		x						
Ceramium byssoideum	Fulton					—																											
	Rockport					—																											
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																				
	Port Aransas		x			—																											
Ceramium fastigiatum f. flaccida	Fulton		x	x		—																											
	Rockport		x,t	t		—																											
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																				
	Port Aransas		x	x		—	x						t	x,t	x,t	x	x	x	x	x					x	x,t	x						
Ceramium strictum	Fulton					—																											
	Rockport					—																											
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																				
	Port Aransas		t			—		x	x					x	x,t	x	t	x,t	x	x					x	x,f t	x,t						
Centroceras clavulatum	Fulton					—																											
	Rockport					—																											
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—											x		x		x	x				
	Port Aransas	x	x,t	x,t		—	x	x	x					x,t	x,t	x,t	t	x,t	x	x	x	x	x	x	x	x,t	x	x					
Spyridia aculeata	Fulton					—																											
	Rockport					—																											
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																				
	Port Aransas		x	x		—									x	x	x,t	x									x	x					
Spyridia filamentosa	Fulton					—																											
	Rockport					—																											
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																			x	x	x
	Port Aransas					—																											
Polysiphonia boldii	Fulton			x,f t	x	—		x	x		x	m,f t	x,f											x	x,t	x	x	x,t				
	Rockport		t	f,t	x	—	x	t	x		x																						
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	x	x			x	x			x	x	m	x	x	x,f						
	Port Aransas		t			—			t									f															
Polysiphonia denudata	Fulton					—																											
	Rockport					—																											
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																				
	Port Aransas					—				m,t	m,t	t	t	x,m t	x,t	x,t	f,t	m,f t	f,t	m,f t	t	x,m f,t	m,t	f,t	m,f	x,m f,t	x,f t						

TABLE 1 (Part 4)

Species	Locality	1967 June	July	Aug	Sep	Oct	Nov	Dec	1968 Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	1969 Jan	Feb	Mar	Apr	May	June	July
Polysiphonia echinata	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—								t	x,f t	x				
	Port Aransas					—																					
Polysiphonia gorgoniae	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	f,t										f,t	f,t	m,f t	f,t
	Port Aransas					—																					
Polysiphonia havanensis	Fulton					—															f	x,f	x,f	t	x,f	x,f	m,f
	Rockport					—																t	t		t	t	t
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—										x				
	Port Aransas					—																					
Polysiphonia subtilissima	Fulton		t			—	x	x	x	x	x	t	x,t	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Rockport					—		x				x,t	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—																					
Polysiphonia tepida	Fulton					—																					
	Rockport		x			—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas		x	x		—		x			x	x	x	x							x		x	x		x	
Bryocladia cuspidata	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas		x,t	f,t	x	—	x,t	t	x,f	x	x,t	m,t	t	t	m,t	t	m,f t	m,f t	x,t	x	x	x	x,t	f,t	f,t	x,t	t
Bryocladia thyrsigera	Fulton					—																					
	Rockport					—																					
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—														
	Port Aransas					—																					f

Digenia simplex	Fulton					—																									
	Rockport		x	m		—																									
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	x	x	x	x	x					
	Port Aransas					—																									
Herpo-siphonia tenella	Fulton					—																									
	Rockport					—																									
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																		
	Port Aransas		x	x		—			x					x		x		x		x							x	x	x,t		
Chondria cnico-phylla	Fulton					—																									
	Rockport					—																									
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—						x	x		x	x,m f,t	x,m f	x,f	x	x				
	Port Aransas					—																									
Chondria dasy-phylla	Fulton					—																									
	Rockport					—																									
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																		
	Port Aransas					—										x															
Chondria littoralis	Fulton		f,t	f		—																		x,t	x,t	f,t	x,t		t		
	Rockport	m,f t	t	t		—					t							x				x	x	f				t		
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—																		
	Port Aransas					—																									
Laurencia poitei	Fulton					—																									
	Rockport					—																									
	Redfish Bay	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x		x		x	x	x	x				
	Port Aransas					—																									

Key to Table 1:
x = vegetative; s = sporangium; p = plurilocular reproductive organ; u = unilocular reproductive organ; m = male; f = female &/or carposporophyte; t = tetrasporangium; c = conceptacle; a = alpha spore; b = beta spore; — = no collection made.

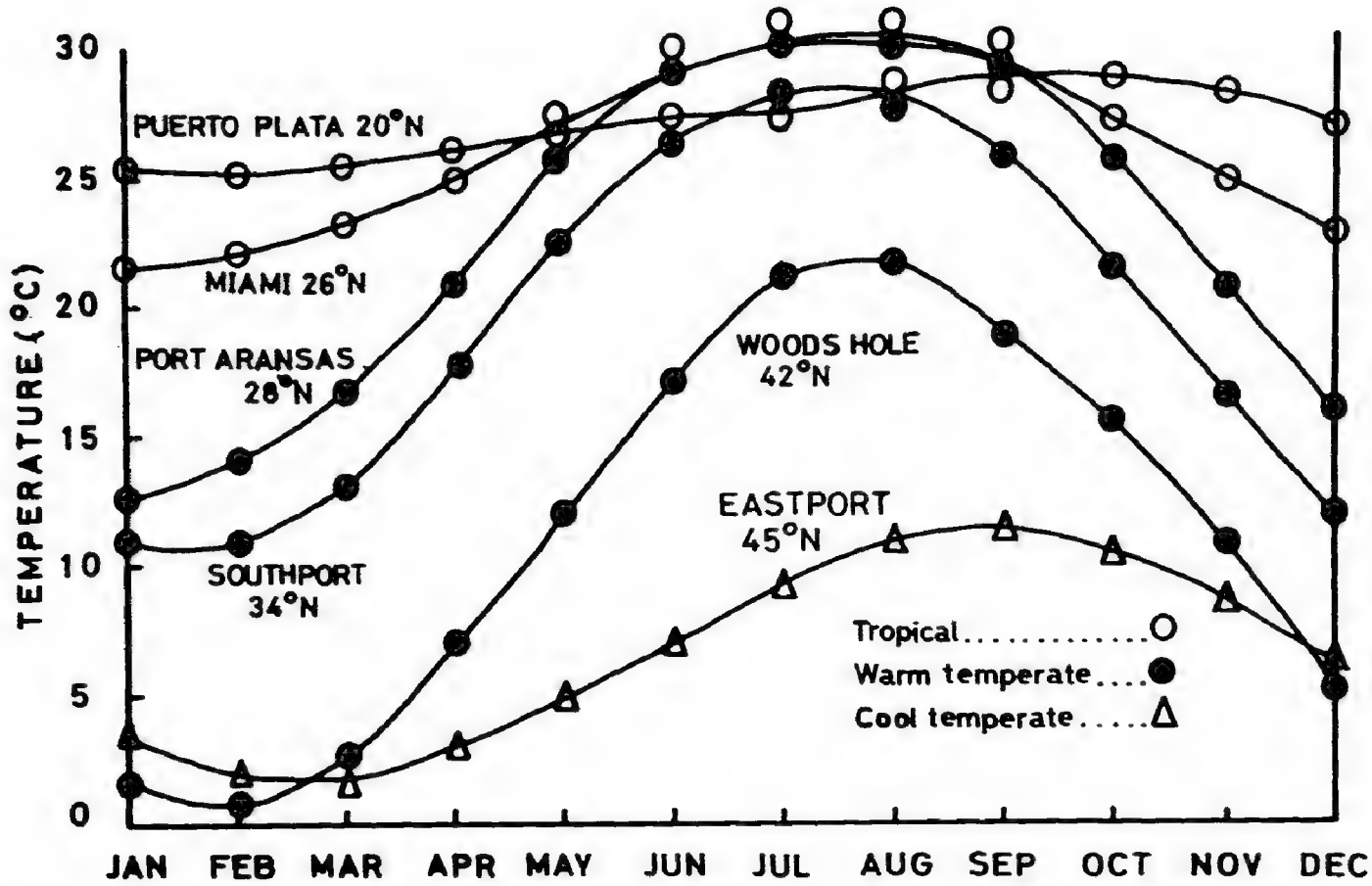


FIG. 2. Mean monthly surface water temperatures at different latitudes along the eastern seaboard of the Americas. Drawn from data obtained from U.S. Dept. Comm. (1965).

June of 645 langleys[1] per day, and an average monthly minimum in December of 256 langleys per day.

3. Daylength

The maximum average monthly daylength of the area was 13 hr 54 min in June and the minimum average monthly daylength was 10 hr 24 min in December. The maximum monthly seasonal difference in daylength was a mere 3.5 hr, but this was shown to be of great significance in effecting a seasonal change in certain taxa in the local flora (Edwards, 1969b).

4. Salinity

The salinity regimes in the area varied tremendously and depended on the rainfall distribution. The climate in the study area is characteristically dry with brief periods of heavy rain, which usually occur in May-June and September (Collier and Hedgpeth, 1950). However, the yearly distribution of rainfall varies widely so that the rainfall, and consequently the salinity variations from year to year, far outweigh the seasonal differences. The salinities in dry to drought years in Aransas Bay are in the range 30–40 ppt, in "normal" rainfall years in the range 20–30 ppt, and in wet years below 20 ppt and even as low as 5 ppt. The salinities in Redfish Bay approximate those at Port Aransas more closely, but since the bay is extremely shallow, salinities tend to be high in summer and may reach 40 ppt in drier years. The salinities fluctuate at Port Aransas but not as extremely as in Aransas Bay. Typical salinity values are as follows: in dry to

[1] langley = 1 gm-cal/cm²-day.

drought years in the middle and upper 30's, in "normal" years in the lower 30's and in wet years in the upper 20's (Parker, 1955; Behrens, personal communication). The present study began during a dry period, but was broken by prolonged torrential rain which accompanied hurricane Beulah in September, 1967. Following the hurricane, salinities as low as 5 ppt were recorded at high tide at Port Aransas and were 15 ppt or lower at high tide for 2 weeks; low tide salinity readings at Port Aransas were below 15 ppt for about 1 month as runoff poured into the bays and thence to the sea. Salinities characteristic of wet years prevailed for most of the study but towards the latter part salinities did rise. Salinity data for the southwest jetty, Port Aransas and for Fulton and Rockport in Aransas Bay are presented graphically in Fig. 5.

5. Tides

The tides in the study comprise two types: diurnal or "tropical" tides with one high and one low each 24-hr period, of maximum range, and mixed or "equatorial" tides with two highs and two lows per day, of minimum range (Fig. 3). During the "equatorial" part of the tidal cycle a loss of phase often occurs to give a "vanishing tide", i.e., a high stand of the sea above mean sea level which lasts from one to several days (Hedgpeth, 1953).

The tidal amplitudes are small. The mean diurnal tidal range (difference in height between mean high water and mean low water level) was only 1.7 ft. in 1967; the maximum high and low water levels were +1.1 and −2.2 ft., respectively, giving a maximum range of 3.3 ft. (U.S. Department of Commerce, 1967).

The tidal patterns of Redfish and Aransas Bays are similar to those of the Gulf, but are dampened with respect to those of the open sea. Winds probably cause the most noticeable fluctuations in water level in the bays because the latter are shallow with only a narrow opening to the sea (Collier and Hedgpeth, 1950).

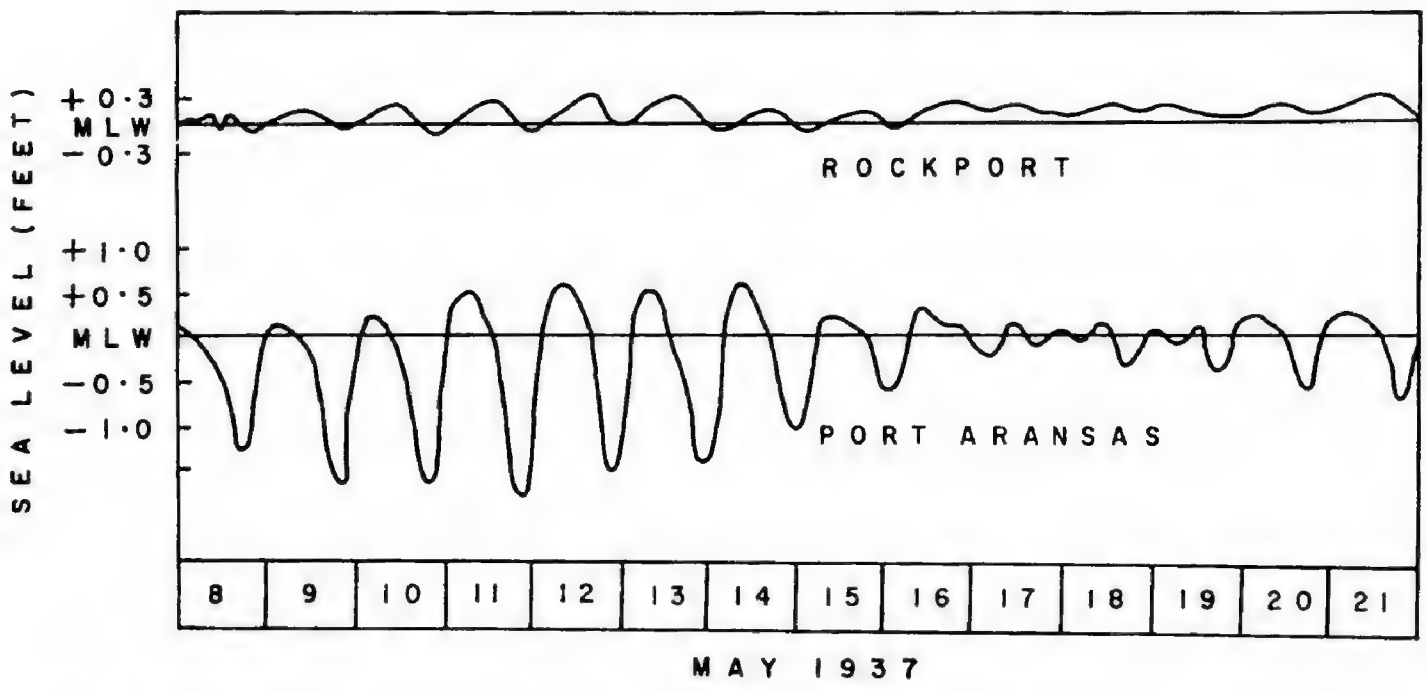


FIG. 3. Tidal curves for Rockport, Aransas Bay & Port Aransas. Redrawn from Collier & Hedgpeth (1950).

Seasonal changes in sea level which are greater than the average daily change take place. The highest average monthly sea levels occur during spring and fall and are called "spring" and "fall-tides," respectively. Thus the tidal zones change four times a year (Marmer, 1954).

6. Wind

The area is subject to much wind, the amount of which is fairly constant throughout the year. The prevailing winds are southeasterlies but during winter frequent "northers" also occur. The southwest jetty is aligned at 122°; thus when the wind is from N.W. to E.S.E. wave action is largely on the northerly side of the jetty and when from S.E. to W.N.W. the wave action is largely on the southerly side of the jetty.

The most pronounced wind effect is the hurricane tide, which can raise water level 15–16 feet in the immediate area of the storm. Hurricane Beulah struck the northeast coast of Mexico less than 320 km from the study area in September 1967 and raised the water level by several feet at Port Aransas.

7. Turbidity

The waters of the area show a great tendency to be turbid. The turbidity is related to runoff water, which transports fine-grained sediments into the bays and then into the sea. Winds agitate the shallow waters of the bays and keep the particulate matter in suspension. Thus the bays generally have a higher turbidity than the Gulf and consequently the water in the pass between the jetties is often less turbid at high tide than at low tide and vice versa. Since turbidity results from rainfall and wind, both of which vary seasonally, the turbidity shows seasonal fluctuations. In general the turbidity is high in summer and low in winter, and during the latter period long periods result when the water is clear. There is a diurnal turbidity in the bays in late spring and summer; the winds are light in the morning and as the land mass warms during the day a thermal wind develops, which increases the turbidity of the water (Conover, 1964). Turbid bay waters absorb and scatter up to 90% of the incident light in the first 10 cm as opposed to only 30% when conditions are relatively calm. After several days of calm weather only 10% is lost in the first 10 cm over *Thalassia* beds (Conover, 1964).

DISCUSSION AND CONCLUSIONS

The earlier records from the study area (the southwest jetty, Port Aransas and Aransas and Redfish Bays) were compiled by Taylor (1935, 1936, 1941), who recorded 32 species. Taylor (1943) later added *Pterocladia americana* to bring the total to 33 species. Humm & Hildebrand (1962) collected 55 species, of which 36 were new to the area so that the total then stood at 69 species. Parker (1964) listed 4 species, 1 new to the area, to make a total of 70 species. Humm (1964) reported *Polysiphonia subtilissima* in the area in a paper on the epiphytes of *Thalassia testudinum* in Florida to bring the total to 71 species. Finally Conover (1964) reported 52 species of which 21 were new to the area to make a total of 92 species. Eighty-nine species were collected during the present study of which

35 were new to the area, so that a total of 127 species have been recorded from the area. However, of the 38 species recorded previously from the area but not collected during the study, 27 are from genera whose taxonomy is confused. Several of the latter are probably conspecific with taxa collected during the study, so that a more realistic total for the number of species that have been found in the study area is probably nearer to 100. Certain species were absent from the area during the study probably because most of the observations were made in hyposaline conditions. A study of the area in dry to drought conditions with concomitant hypersaline conditions would almost certainly reveal some of the "missing" species.

The results are discussed in terms of the spatial (large scale horizontal or geographical, small scale horizontal or local, and vertical distribution) and seasonal distribution of the flora.

Geographical Distribution and Floristic Affinity

Temperature is the major factor controlling the geographical distribution of marine algae and has been used as the parameter for the division of the oceans into biogeographic zones. Setchell (1915, 1920b) divided the surface waters of the Northern Hemisphere into five zones, based on surface water isotherms (maximum average monthly water temperatures). Each zone covered a range of 5°C, except the polar region which included a range of 10°C: upper boreal, 0–10°; lower boreal, 10–15°C; north temperate, 15–20°C; north subtropical, 20–25°C; and tropical, 25–30°C. He considered that there was a correspondence between the isotherms for surface water temperatures and the boundaries of different marine floras. He observed that most species of algae have a narrow temperature range for "normal persistence." Where large seasonal variations in temperature occur, for example in the temperate and subtropical zones of Setchell, the species "normal" to the zone endure the colder portion of the year in a state of quiescence, vegetatively or as a spore stage. Species of a "lower zone" invade the zone during the colder season, and pass into quiescence when the characteristic temperature of the zone prevails again during the summer (Setchell, 1920a). Setchell clearly recognized the varying temperature responses of algae from different geographical areas, but his boundaries do not coincide with the known boundaries of algal distributon. Furthermore, his system, based on mean temperature maxima for the summer months with the concept of "stenothermy and zone invasion" as outlined above, does not adequately emphasize the dual nature of the flora of the mid-Atlantic and northern Gulf of Mexico coasts of North America.

Stephenson and Stephenson's (1952, 1954) division of the eastern coast of North America into biogeographic zones stresses the distinct seasonal alteration of the algal vegetation and corresponds closely to the seasonal temperature changes along the coast as outlined by Parr (1933). Southern Florida has a relatively small seasonal temperature range and relatively warm water year round. To the north of Cape Cod the waters again have a relatively small seasonal temperature range, but with relatively cool water year round. Wide seasonal ranges

in temperature occur, however, between Cape Cod and Cape Kennedy, Florida. A seasonal water temperature barrier is established at Cape Cod each summer, so that only a gradual decline in water temperature takes place in summer, moving northwards from the south to Cape Cod. Each winter a seasonal temperature barrier is established at Cape Hatteras, so that cool water penetrates south (Parr, 1933). Cool winter water temperatures from Cape Hatteras to Cape Kennedy and in the northern Gulf of Mexico are largely associated with cool air temperatures at this time.

The Stephensons (1952, 1954) call the most northerly part of the Atlantic coast of the United States, north of Cape Cod, a cool temperate region, with the mean warmest month between 10–20°C, and well below 10°C in winter but not usually less than 0°C on the open coast. The region is characterized by well developed fucoid and laminarian zones. Cape Cod southward to Cape Hatteras is an intermediate region where fucoid and laminarian zones gradually weaken, and the red algae of southern affinity increase in number. Cape Hatteras to Cape Kennedy, including the northern Gulf of Mexico, is a warm temperate region with minimum winter sea temperatures 10–20°C and summer maxima near 25°C. It is characterized by a large increase of red algae and a decrease in brown algae compared to the cool temperate region. The algal population lacks the most stenothermal tropical and cold water forms, but includes eurythermal tropical and cold water species which fluctuate with the season. The most southerly portion of the eastern coast of North America from Cape Kennedy to the Florida Keys is a tropical region, with winter temperatures not much below 20°C, and the summer ones 25°C or above; red algae dominate the flora.

Humm (1969) discussed the distribution of algae along the Atlantic coast of North America. He considered that the flora was made up of only two major geographic floral units. One of the units originated, and is centered, in the tropical Caribbean and has its major inshore northern boundary at Cape Kennedy. The other unit originated, and is centered. in the temperate cool waters of the upper north Atlantic and has its major inshore southern boundary at Cape Cod. He considered the coast line from Cape Kennedy to Cape Cod, including the northern shore of the Gulf of Mexico, to be "a vast transition zone occupied . . . by the more eurythermal elements of each major flora."

The geographical distribution of 78 species[1] in the local flora on the west Atlantic coast from Canada to the Caribbean are presented diagrammatically in Fig. 4 and were used to determine the floristic affinity of each species. Nine species (11.5%) range from Canada to the southern United States and are thus of cool temperate north Atlantic affinity. Forty one species (52.5%) range from the Caribbean to various areas in the United States and are thus of tropical Caribbean affinity. Two species (2.6%), *Rhodymenia pseudopalmata* and *Polysiphonia echinata*, range from tropical south Florida into warm temperate waters and are probably of tropical Caribbean affinity although they have not been reported

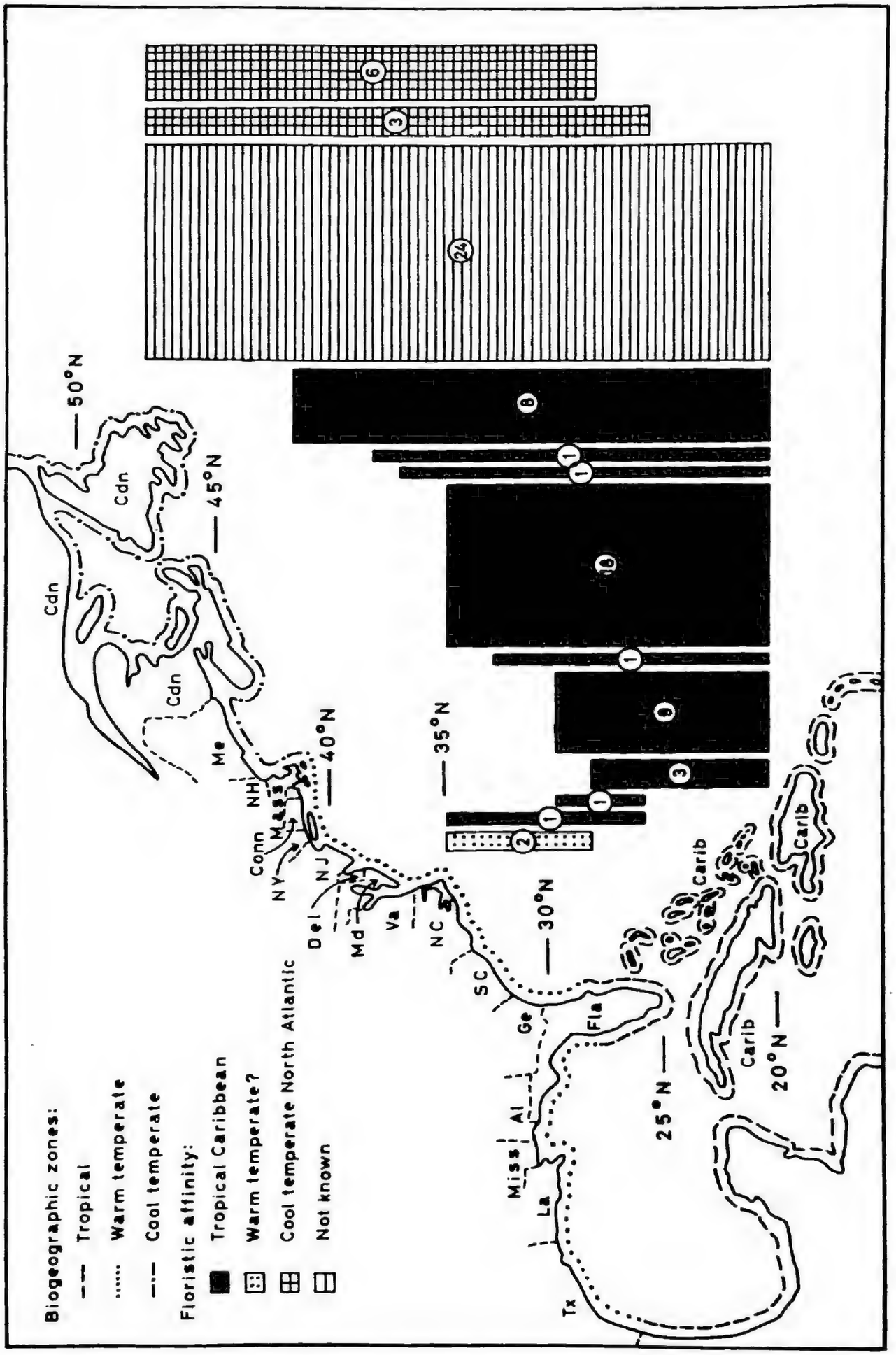
[1] The geographical distributions of the following 11 species were not determined: *Cladophora albida, C. dalmatica, C. delicatula, C. ruchingeri, Agardhiella baileyi, A. tenera* (taxonomy confused); *Sargassum fluitans, S. natans* (pelagic species); *Streblonema* sp., *Spermothamnion* sp. (specific identity unknown); *Polysiphonia boldii* (recorded only from Texas).

from the Caribbean. Two species (2.6%), *Acrochaetium hoytii* and *Polysiphonia tepida*, have been reported only from warm temperate waters but their restricted distribution is probably a reflection of inadequate collecting and further data should extend their ranges into the tropics. The floristic affinity of 24 species (30.8%) could not be determined from their geographical distribution since they extend from Canada to the Caribbean; these are very eurythermal species which can tolerate tropical to cool temperate waters. Their floristic affinity, however, can often be deduced from a consideration of their seasonal distribution at different latitudes (see next section). Thus the largest group of species in the flora consists of warm eurythermal species of tropical Caribbean affinity. The northern limit of most of these species, which is situated further north as the eurythermality increases, is at Cape Kennedy, Cape Hatteras or Cape Cod (Fig. 4). This distributional pattern can be correlated with the surface temperature of inshore coastal waters and provides additional evidence for the relationship between temperature and the geographical distribution of marine algae.

Seasonal Distribution at Different Latitudes

Correlations were sought between the seasonal distribution of species in the local flora and their geographical range from Canada to the Caribbean and variations in certain environmental factors, in an attempt to determine which factors control the growth of benthic marine algae. Seasonal temperature variations are slight in tropical and small in cool temperate waters but are considerable in warm temperate waters (Fig. 2). Summer temperatures in the latter region approximate those of tropical waters while winter temperatures are similar to those found in cool temperate regions in summer. Seasonal daylength variations are negligible at the equator and increase in magnitude towards the poles (Fig. 6). The differences in light intensity in summer between various latitudes are small but in winter the values fall as the latitude increases (Fig. 7). Feldmann (1938) compared the seasonal periodicity of algal vegetation on the east coast of the north Atlantic in the English Channel and in the Mediterranean. *Arthrocladia villosa*, an alga from deep water where temperature variations are small, developed only during the summer in both regions. The absence of the species in winter was attributed to weak light at that time. *Ulothrix flacca* occurred throughout the year in the English Channel and in winter and spring in the Mediterranean, while *Padina pavonia* grew throughout the year in the Mediterranean but only in summer in the English Channel; these two species were thus considered to be cold and warm water species, respectively.

The local species can be divided largely into two main categories with regard to their seasonal distribution at different latitudes: group 1 in which the seasonal distribution varies with latitude, and group 2 in which the seasonal distribution is similar at different latitudes (Table 2). The seasonal distribution of algae in group 1 is probably determined primarily by temperature, and can be subdivided further into sections 1A and 1B depending on whether growth is inhibited by low or elevated water temperatures, respectively. Group 1A comprises warm eurythermal species of tropical Caribbean affinity, e.g., *Padina vickersiae* and *Centro-*


6
3
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Mass
Conn
NY
NJ
Del
Md
Va
NC
SC
Ga
Fla
Miss
Al
La
Tx
Carib
Carib
Carib
Biogeographic zones:
Tropical
Warm temperate
Cool temperate
Floristic affinity:
Tropical Caribbean
Warm temperate?
Cool temperate North Atlantic
Not known

TABLE 2

The seasonal distribution of the local species at different latitudes

GROUP 1		GROUP 2
Seasonal distribution varies with latitude		Seasonal distribution similar in different latitudes
A Warm eurythermal species	B Cold eurythermal species	Cold eurythermal—daylength sensitive species
Perennial with/without summer-autumn growth maximum (occasionally present in summer-autumn) in the south but summer-autumn occurrence (occasionally perennial with/without summer-autumn growth maximum) in the north.	Winter-spring occurrence or perennial with winter-spring growth maximum in the south but perennial with/without summer-autumn growth maximum or summer-autumn occurrence in the north.	Winter-spring occurrence; certain species extent into summer or are perennial in north but demonstrate a winter-spring growth maximum.

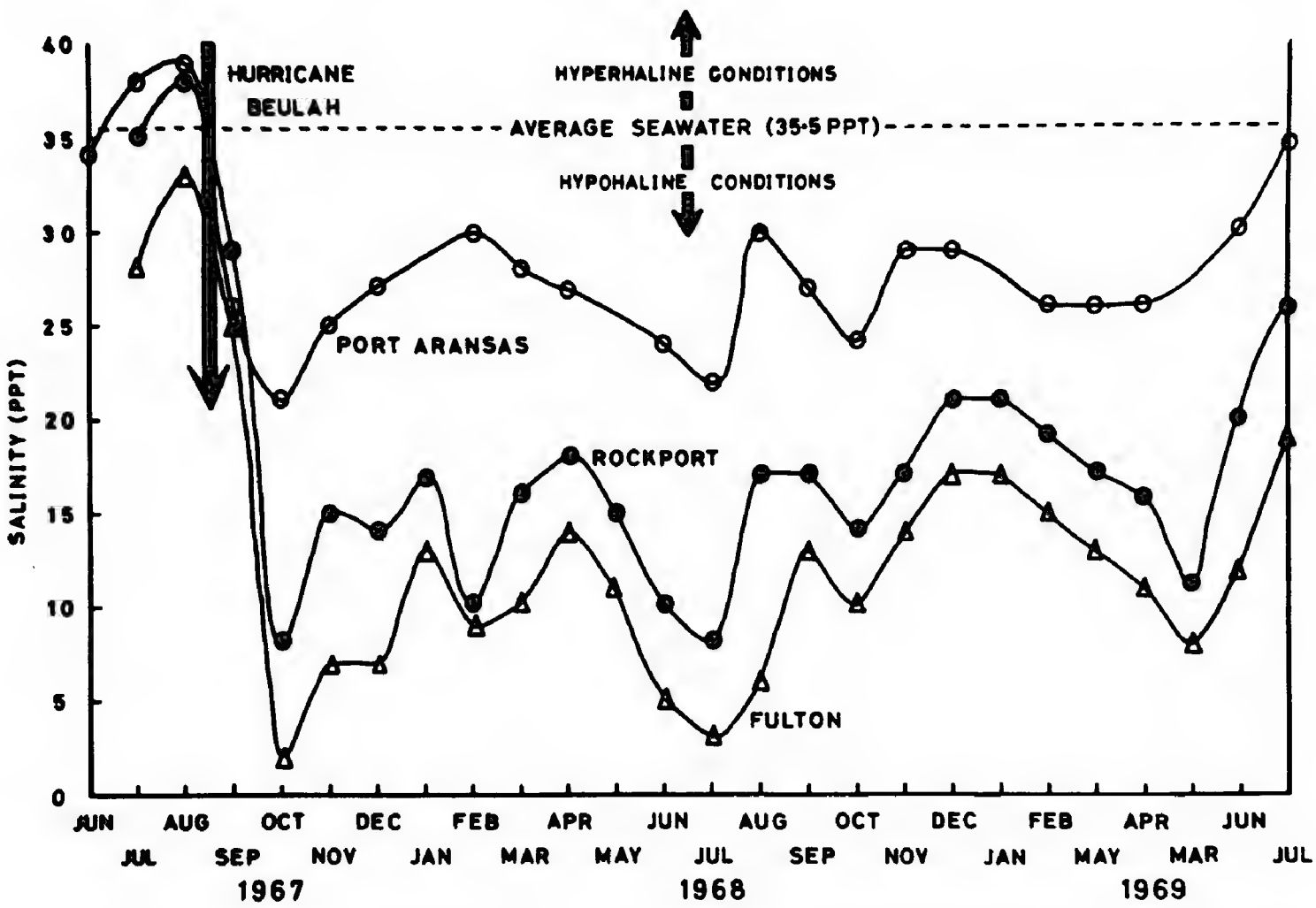

FIG. 5. Monthly salinity values for Fulton, Rockport ,Aransas Bay and the southwest jetty, Port Aransas during the study. The Aransas Bay values are an average of 1–2 readings, those at Port Aransas an average of 10–58 readings.

FIG. 4. The floristic affinity of the Port Aransas flora based on the geographical distribution of the species. The vertical axes of the histograms represent the geographical distribution of the local species and the width of the horizontal axis is proportional to the number of species in each floristic group (the actual number of species in each group is also indicated in the histogram).

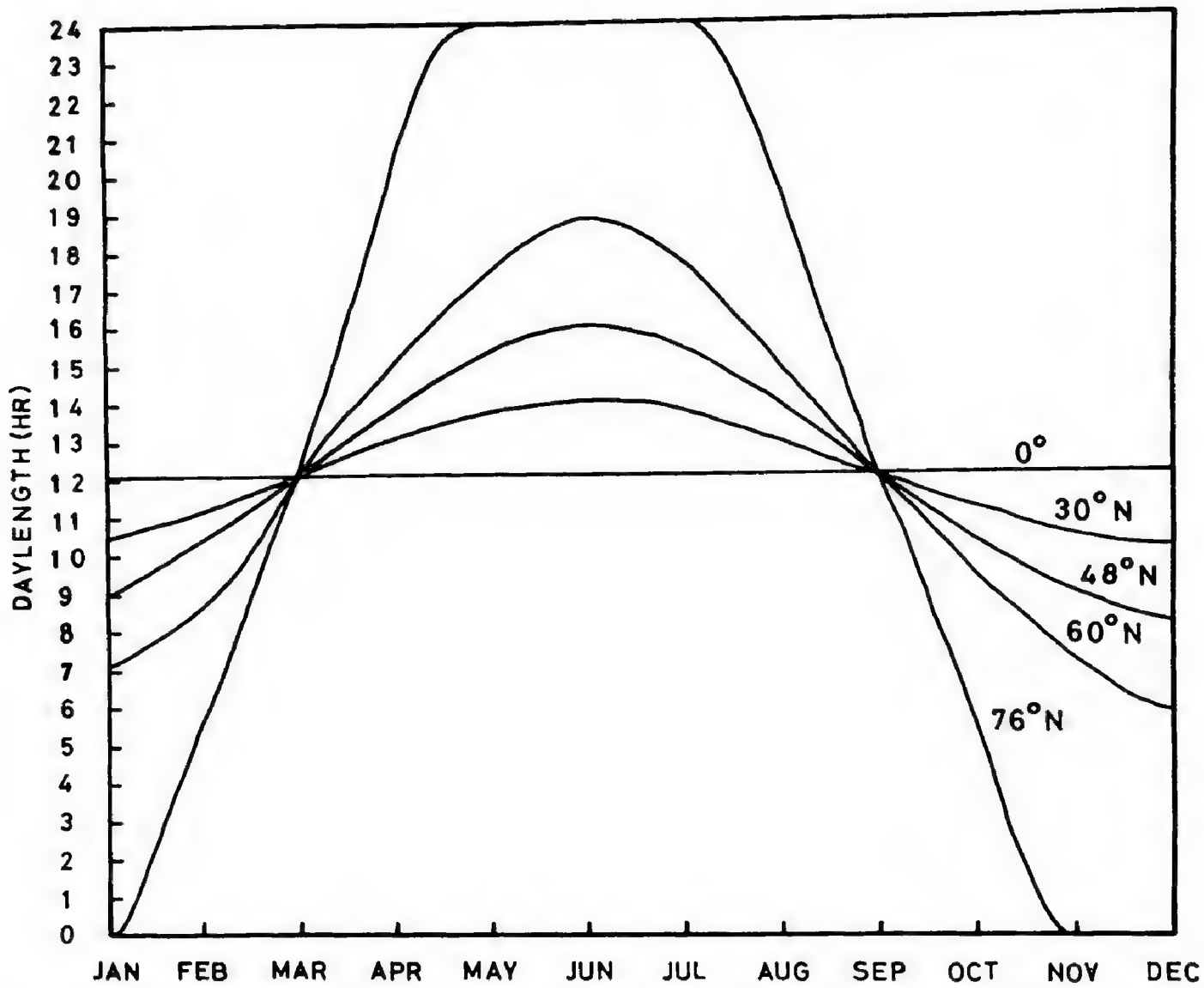

FIG. 6. Seasonal daylength variations at different latitudes. Drawn from data obtained from U.S. Dept. Comm. (1967).

ceras clavulatum. Certain species which range from the Caribbean to Canada demonstrated a similar variation in seasonal distribution, e.g., *Gracilaria foliifera* and *Polysiphonia denudata*. These species are restricted to sheltered, shallow-water localities in cool temperate waters where the water is warmer than that of the surrounding coast (Taylor, 1957; Setchell, 1922), which indicates also that they are eurythermal warm water algae of tropical Caribbean affinity. Elevated summer water temperatures which can exceed 30°C in shallow bays in warm temperate and tropical waters may also inhibit growth as Phillips (1960b) suggested in central Florida. Group 1B consists of cold eurythermal species of cool temperate north Atlantic affinity, e.g., *Ectocarpus siliculosus* and *Stictyosiphon subsimplex*. Certain species which range from Canada to the Caribbean but demonstrated a similar seasonal distribution are probably also of cool temperate north Atlantic affinity, e.g., *Entermorpha clathrata* and *Ulva lactuca*.

The algae in group 2 demonstrate a similar seasonal distribution, a winter-spring occurrence, in areas of varying temperature and light intensity regimes which suggests that their growth may be controlled by daylength variations. The species in the group are of cool temperate north Atlantic affinity, e.g., *Ulothrix flacca*, *Petalonia fascia* and *Bangia fuscopurpurea*. Since certain species extend into the summer and may even be perennial in the north a low water tempera-

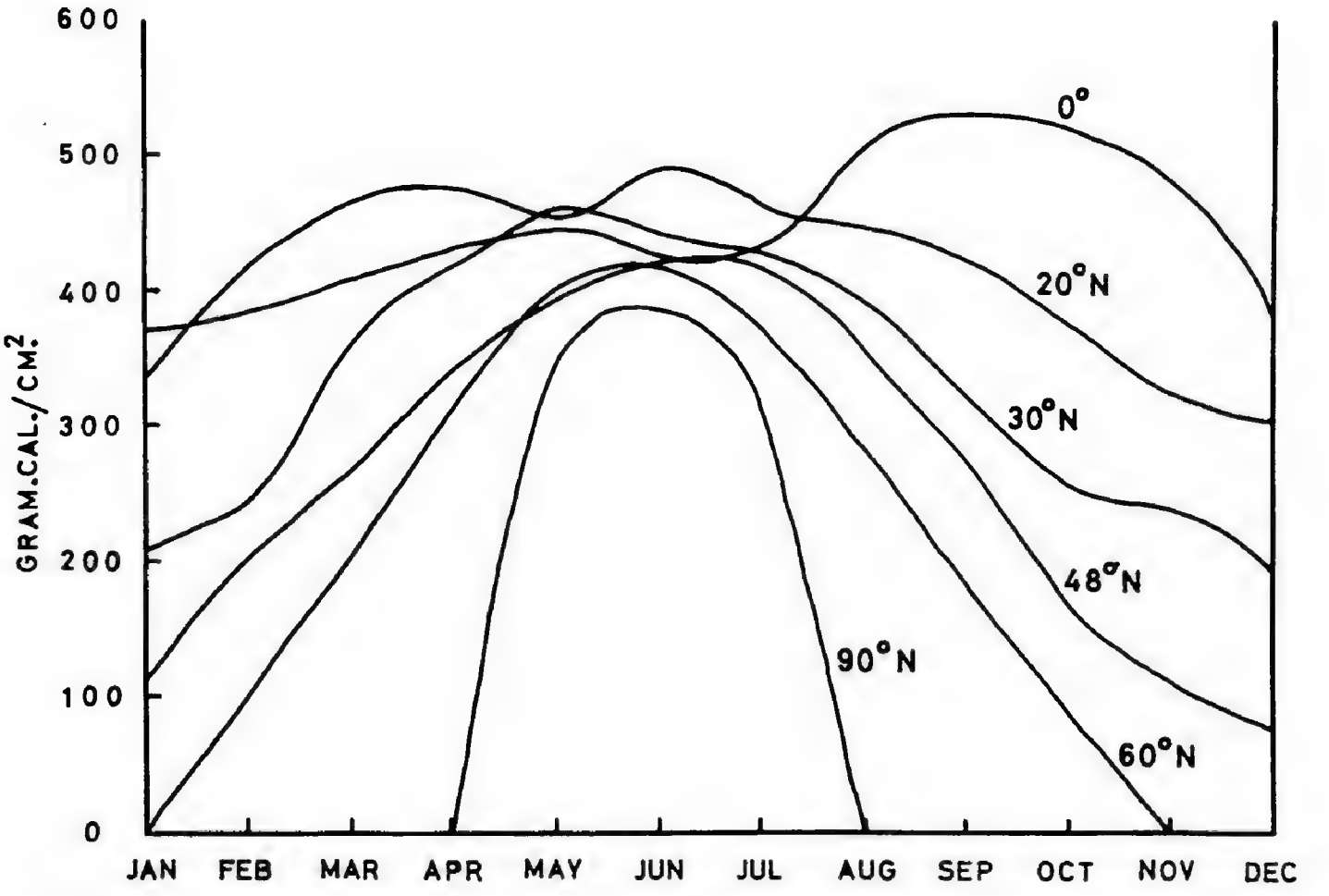

FIG. 7. Seasonal variation in solar radiation at different latitudes. Drawn from data obtained from Kimball (1928).

ture is probably also involved as a controlling factor in growth, as was demonstrated in culture for *Petalonia fascia* and *Porphyra leucosticta* by Edwards (1969b).

A third, smaller group comprises certain species which have been recorded only in warm temperate and tropical water and are thus of tropical Caribbean affinity and yet occur only during winter and spring in warm temperate waters, e.g., *Cladosiphon occidentalis* and *Polysiphonia echinata.* Their seasonal distribution of growth indicates that they may be responding to variations in daylength, but it is difficult to understand how the growth of a species of tropical affinity could respond to daylength variations, since the daylength is relatively constant throughout the year in equatorial regions.

R/P Ratio

There is a progressive diminution of the percentage of brown algae and an increase in the percentage of red algae in the flora of a given area proceeding from arctic to tropical waters (Feldmann, 1938). The ratio of red to brown algae (R/P ratio) is almost unity in arctic regions and increases to over 4 in the tropics. The flora of the Port Aransas area has a relatively high R/P ratio of 3.8, which demonstrates further that the floristic affinity is close to that of the tropics.

Disjunct Distribution

The warm temperate flora of the northern Gulf of Mexico is related to that of

TABLE 3

Species with a disjunct distribution in the local flora

Ectocarpus siliculosus
Streblonema oligosporum
Petalonia fascia
Bangia fuscopurpurea
Porphyra leucosticta
Acrochaetium hoytii[1]
A. virgatulum[1]
Polysiphonia tepida[1]

[1] Species with maximum development during the summer months, and probably of tropical Caribbean affinity. Their apparent disjunct distribution is probably due to inadequate collecting in the tropical Americas.

the Atlantic coast between Cape Cod and Cape Kennedy but at present is isolated from it by the tropical waters of south Florida. Most species common to the two warm temperate floras are distributed continuously around the Florida peninsula but the species in Table 3 are disjunct in their distribution and do not occur in the intervening tropical waters of south Florida.

The disjunct species are largely of cool temperate North Atlantic affinity and occurred in the study area only during winter and spring. The year-round elevated water temperatures of south Florida probably contribute to the absence of these algae from that area. Their distribution was probably continuous in the past. Sea temperatures were lower in the Pleistocene so that the algae possibly had a continuous distribution but became separated as water temperatures rose after the end of the epoch. During the interglacial periods of the Pleistocene the Florida peninsula was submerged and the waters of the northern Gulf of Mexico were confluent with those of the Atlantic across northern Florida; the two parts of the present warm temperate flora were possibly subsequently isolated as the sea level fell and Florida emerged (Hedgpeth, 1953; Humm and Caylor, 1957). The discontinuous species may have become established in the northern Gulf of Mexico in relatively recent times; the flow of the Gulf Stream in a northerly direction off the southeast coast of the United States eliminates the agency of ocean currents as a causal factor, but they may possibly have been transported on the hulls of ships or in ballast tanks.

Local Distribution

The number of species (those that were collected on at least 6 occasions during the study) recorded from each of the three localities was as follows: southwest jetty, Port Aransas 48 species; Aransas Bay 34 species; and Redfish Bay 29 species. Thus the southwest jetty was more favorable than the bays for algal growth when the flora was considered as a whole. However, when the local distribution of individual species was considered, it was found that all seven possible permutations of distribution between the three localities occurred (Table 4), which suggests that the local species had widely varying habitat requirements; e.g., *Enteromorpha clathrata* and *Gracilaria foliifera* were ubiquitous and thus tolerant of the range of environmental conditions in the area during the

TABLE 4

Horizontal distribution of the local species[1]

One locality	Two localities	Three localities
S.W. Jetty, Port Aransas	S.W. Jetty, Port Aransas	S.W. Jetty, Port Aransas,
Ulva fasciata	& Aransas Bay	Aransas Bay & Redfish Bay
Cladophora albida	Enteromorpha ramulosa	Entocladia viridis
Bryopsis hynoides	Ulva lactuca	Enteromorpha clathrata
Giffordia indica	Cladophora dalmatica	E. flexuosa
Petalonia fascia	Padina vickersiae	E. lingulata
Bangia fuscopurpurea	Goniotrichum alsidii	Cladophora delicatula
Porphyra leucosticta	Erythrocladia subintegra	C. vagabunda
Pterocladia capillacea	Acrochaetium trifilum	Giffordia mitchelliae
Corallina subulata	A. flexuosum	G. rallsiae
Agardhiella tenera	Gelidium crinale	Dictyota dichotoma
Rhodymenia pseudopalmata	Grateloupia filicina	Erythrotrichia carnea
Callithamnion byssoides	Ceramium fastigiatum	Hypnea cornuta
Spermothamnion sp.	f. flaccida	H. musciformis
Ceramium strictum	Polysiphonia tepida	Gracilaria foliifera
Spyridia aculeata	S.W. Jetty, Port Aransas	Polysiphonia boldii
Polysiphonia denudata	& Redfish Bay	
Bryocladia cuspidata	Chaetomorpha linum	
Herposiphonia tenella	Dermatolithon pustulatum	
Aransas Bay	Corallina cubensis	
Polysiphonia havanensis	Centroceras clavulatum	
P. subtilissima	Aransas Bay & Redfish Bay	
Chondria littoralis	Acetabularia crenulata	
Redfish Bay	Ectocarpus siliculosus	
Acrochaetium virgatulum	Myriotrichia subcorymbosa	
Heteroderma lejolisii	Digenia simplex	
Gracilaria debilis		
G. verrucosa		
Chondria cnicophylla		
Laurencia poitei		

[1] Species were considered only if they were collected on at least 6 occasions.

study, but *Polysiphonia havanensis* and *Gracilaria debilis* were collected only in Aransas and Redfish Bays, respectively, and thus had relatively narrower habitat requirements. An attempt was made to assess the environmental requirements of each species by a consideration of their horizontal distribution in the area and the environmental conditions in the different habitats.

The major boundaries to the horizontal or local distribution of benthic marine algae in a given area are (1) salinity, (2) nature of the substratum, and (3) degree of wave action.

Salinity

The coastal waters of Texas have salinities which fluctuate widely above or below that of average seawater (35.5 ppt) and are brackish according to the definition of Den Hartog (1967): "brackish water is water with an unstable salinity and the salt of which originates mainly from the sea."

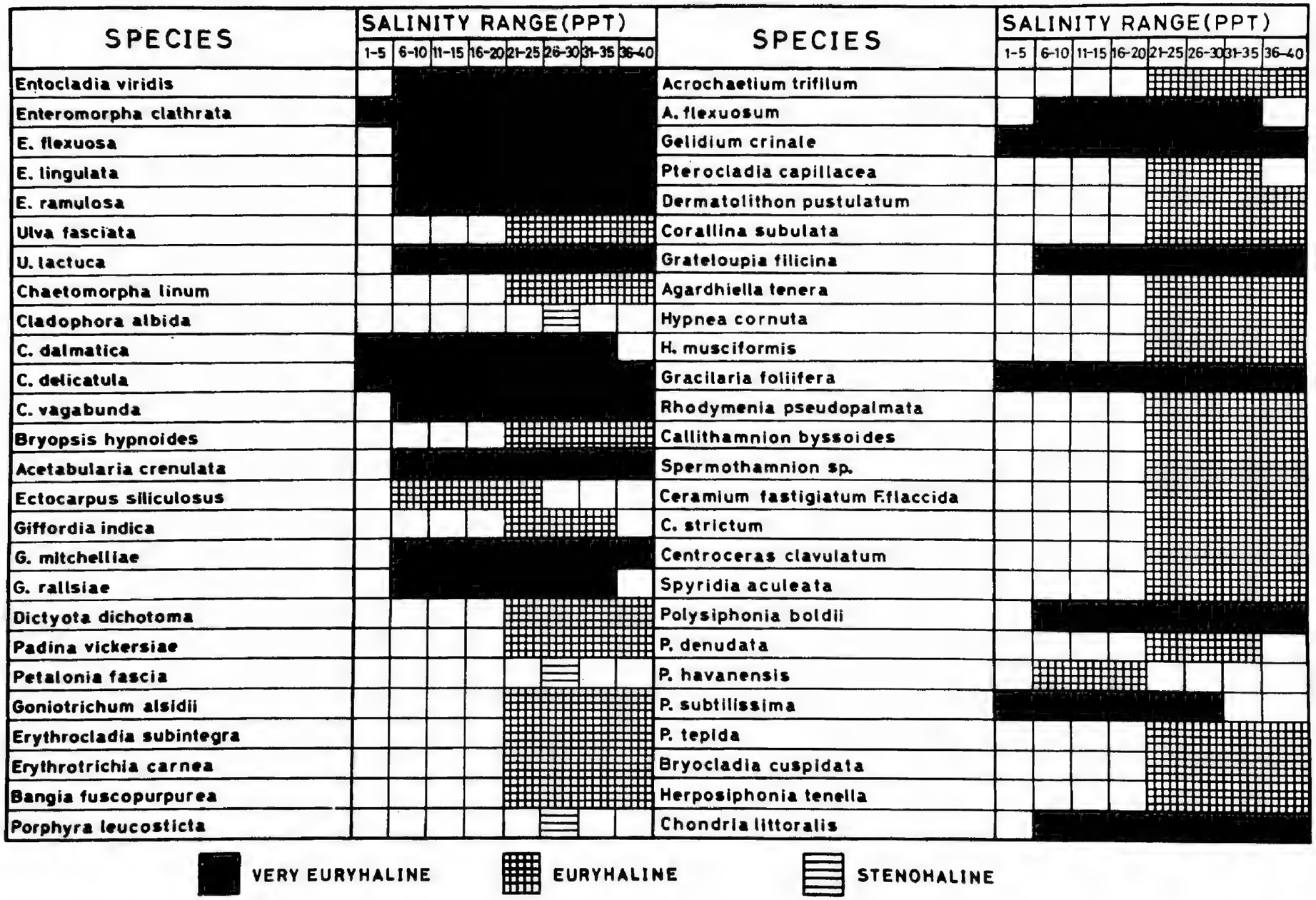

Fig. 8. The salinity ranges of the local species during the study.

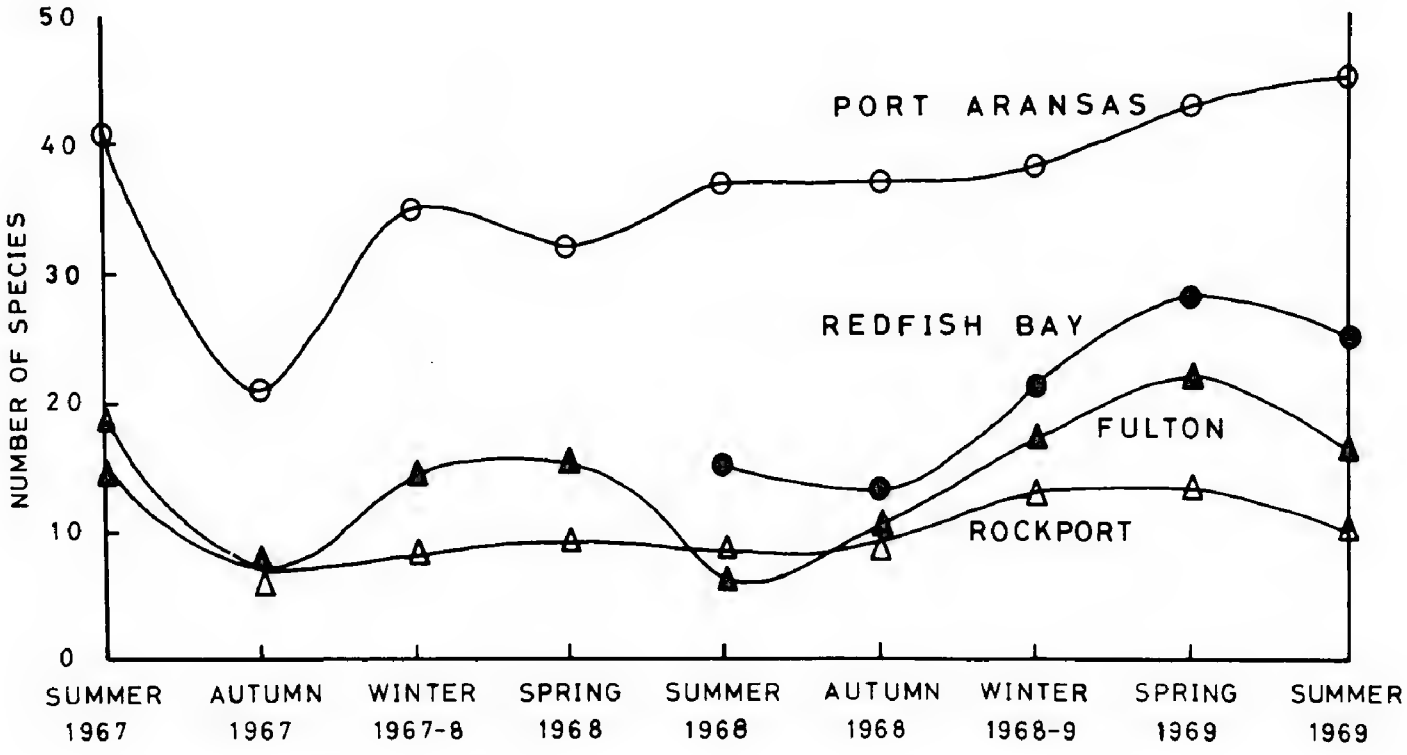

FIG. 9. The species diversity at each station on a monthly basis during the study.

The flora of brackish water is poor in species compared to the stenohaline marine environment. Few freshwater algae can tolerate water containing traces of salt and true brackish species (those which generally do not occur in the sea or in freshwater) are few in number. The majority of species present in brackish water are euryhaline marine species which possess osmotic resistance to large changes in the concentration of seawater (Doty & Newhouse, 1954; Gillham, 1957; Den Hartog, 1967).

The salinity ranges of certain species[1] collected during the study are presented in Fig. 8. The species have also been grouped into three categories according to their degree of tolerance of salinity variations. Stenohaline species occurred in a salinity range of 10 ppt or less, euryhaline species in a range of 11–20 ppt, and very euryhaline species in a range of 21–40 ppt.

The species diversity at each locality throughout the study is shown in Fig. 9. The number of species generally increased with a rise in salinity at each station. A sudden decrease in species diversity following hurricane Beulah in September 1967 was particularly evident. The large reduction in number and biomass of species was probably brought about largely by wave action, but the great reduction in salinity occasioned by Beulah was probably also a causal factor. Parker (1955) demonstrated a relationship between salinity and invertebrates in Aransas Bay, where an invasion of open Gulf of Mexico invertebrates into the bay occurred as the salinity increased. Williams (1949) discussed the effect of salinity fluctuations on algal growth in North Carolina. Unusually high precipitation occurred in spring-summer 1946 and abnormally low precipitation in the same

[1] Species have been considered from Aransas Bay and the southwest jetty, Port Aransas (no salinity data for Redfish Bay) which were collected on at least 6 occasions. This probably excluded possible stenohaline species from relatively high salinity water, since the latter occurred only at the start and conclusion of the study, e.g., *Bryocladia thyrsigera, Pterocladia bartlettii* and *Spyridia aculeata.*

seasons in 1947 with concomitant salinity changes. Places where algae thrived in the latter year were bare or supported a moribund flora in the former year. Similarly, during the present study the number and density of species was reduced in the summer of 1968 relative to those of 1967, presumably due to salinity changes.

The majority of species were euryhaline, which was to be expected in an environment in which salinity varied so widely. *Pterocladia bartlettii* was the only species found prior to hurricane Beulah which was not subsequently collected during the study, and was possibly absent because salinities were too low. The greater part of the study was conducted when the salinity regimes in the study area were below that of average seawater; thus little information was obtained when salinities are above that of average seawater which occurs in dry to drought years. The three stenohaline species, *Cladophora albida, Petalonia fascia* and *Porphyra leucosticta* (Fig. 8) occurred only on the southwest jetty, Port Aransas, during winter and spring. Thus their stenohaline nature may be more apparent than real since during both years the salinity regimes were similar at that time.

Boyle & Doty (1949) demonstrated that certain algae could tolerate reduced salinities better if the temperature were lowered. Wood and Palmatier (1954) and Conover (1958, 1964) made observations which possibly support the hypothesis. According to the hypothesis, perennial algae in Texas would be able to penetrate further into the bays in winter than in summer during hyposaline conditions, but since comparable salinities during summer and winter were not attained, the hypothesis could not be tested in the study area.

Nature of the substratum

Some algae were attached only to solid substrata such as rocks, concrete structures or wooden pilings during the study, e.g., *Gelidium crinale* and *Rhodymenia pseudopalmata.* Others were catholic with regard to choice of substratum and grew on solid substrata and epiphytically on algae or seagrasses, e.g., *Ectocarpus siliculosus* and *Giffordia mitchelliae.* Many species however were epiphytic only. The majority demonstrated very little host specificity, e.g., *Erythrocladia subintegra* and *Acrochaetium trifilum*; but certain species were confined to one or two host species, e.g., *Myriotrichia subcorymbosa* and *Acrochaetium hoytii.* Humm (1964) studied the algal epiphytes of *Thalassia testudinum* and divided them into three groups based on the importance to the alga of the seagrass as a substratum, viz., algae found exclusively or almost so on seagrasses, those common on seagrasses but occurring also on other hosts or non-living substrata, and those present only fortuitously on seagrasses.

Unattached algae on an open coast would be soon washed out to sea or left stranded on the upper shore to perish. However, in the quiet shallow waters of tidal or grass-flats, extensive communities of unattached or loosely attached seaweeds often develop. (Den Hartog, 1959; Phillips, 1959, 1960a, 1960b, 1961). Redfish Bay supported a "floating algal community" comprising species such as *Gracilaria verrucosa, Digenia simplex,* and *Chondria cnicophylla.* The algae were often attached to small shells, but since the substratum had a low specific gravity, they were easily moved by water movements.

Degree of Wave Action

The importance of wave action on algal vegetation was demonstrated by Kingsbury (1962), who conducted a study on a jetty at West Falmouth, Mass., where wave action was essentially the only varying environmental factor; more species were found on the windward than on the leeward side of the jetty. Wave action can change the morphology of certain species. *Fucus vesiculosus* typically possess air bladders, but these are absent in forms from very exposed shores (Burrows and Lodge, 1952). The flattening of the axes of *Gelidium crinale* and *Gracilaria foliifera* on the southwest jetty, Port Aransas was probably due to the greater degree of wave action than in Aransas Bay.

A sudden decrease in number and biomass of species occurred after hurricane Beulah in September 1967 (Fig. 9) which was probably largely due to the scouring action of the accompanying tidal wave. Conover (1958) and Glynn, Almodovar and Gonzalez (1964) both reported the destruction of algal vegetation by hurricanes in southern New England and Puerto Rico, respectively.

Blooms

Blooms, the sudden appearance of certain species of algae in large amounts which then dominate the community for a relatively short time, followed by a sudden decline are common in planktonic organisms. Benthic marine algal blooms, however, were observed during the study. *Giffordia mitchelliae* occurred in bloom proportions on the channel side of the landward end of the southwest jetty, Port Aransas during late autumn and early winter 1967, possibly as a result of a higher nutrient content of the water following hurricane Beulah. *Hypnea musciformis*, *Spyridea filamentosa* and *Chaetomorpha linum* were present in bloom proportions in succession in May, June, and July 1969, respectively, in Redfish Bay.

Changes in the Flora in Different Years

The appearance of the algal vegetation in most areas is generally similar from year to year, since the environmental factors that control the occurrence of algae occur in regular annual cycles. Slight fluctuations in environmental factors are probably important only for species at their limits of distribution. Fritsch (1906) distinguished between regular periodic changes, which recur each year in a seasonal cycle, and irregular periodic changes which take place at any season and have no pattern of occurrence. Distinctive differences were observed in the algal vegetation in the Port Aransas area between the two years of the study, especially in Aransas Bay (Fig. 9). The differences were brought about largely by irregular salinity changes and by the action of the tidal wave of Hurricane Beulah. Thus a distinctive character of the flora of the area was its irregularity. Changes in species composition and abundance from one year to the next were also reported in Massachusetts (Conover, 1958), North Carolina (Williams, 1949), and in Florida (Phillips, 1961).

The Flora of the Southwest Jetty, Port Aransas

The Port Aransas jetties were constructed between 1879 and 1909, and together with pier posts, sea walls, and bridge supports provided a relatively new habitat of hard substrata. Previously the shore consisted of unconsolidated sand and mud sediments, and the only natural substrata were provided by shells, seagrasses, and the algae themselves. Seventeen species (19.1%) were collected only on the southwest jetty which thus constitutes a distinctive algal habitat (Table 5). (Several species were probably relatively stenohaline and were thus restricted to the jetty during the study because salinities were higher than in the bays, where they occur possibly during dry periods when salinities are higher). Where did these species come from to colonize the jetties?

TABLE 5

The seasonal periodicity of growth[1]

Throughout the year	Period of maximum growth Winter-spring	Summer-autumn
Entocladia viridis	Enteromorpha clathrata	Enteromorpha lingulata
Cladophora dalmatica	E. flexuosa	Ulva fasciata
C. vagabunda	E. ramulosa	Chaetomorpha linum
Giffordia indica	Ulva lactuca	Cladophora delicatula
G. mitchelliae	Cladophora albida	Bryopsis hypnoides
G. rallsiae	Ectocarpus siliculosus	Acetabularia crenulata
Acrochaetium flexuosum	Myriotrichia subcorymbosa	Dictyota dichotoma
Gelidium crinale	Petalonia fascia	Padina vickersiae
Pterocladia capillacea	Bangia fuscopurpurea	Goniotrichum alsidii
Dermatolithon pustulatum	Porphyra leucosticta	Erythrocladia subintegra
Corallina subulata	Polysiphonia havanensis	Erythrotrichia carnea
Grateloupia filicina		Acrochaetium trifilum
Hypnea musciformis		A. virgatulum
Gracilaria foliifera		Heteroderma lejolisii
Polysiphonia denudata		Corallina cubensis
P. subtilissima		Agardhiella tenera
Chondria cnicophylla		Hypnea cornuta
C. littoralis		Gracilaria debilis
		G. verrucosa
		Rhodymenia pseudopalmata
		Callithamnion byssoides
		Spermothamnion sp.
		Ceramium fastigiatum f. flaccida
		C. strictum
		Centroceras clavulatum
		Spyridia aculeata
		Polysiphonia boldii
		P. tepida
		Bryocladia cuspidata
		Digenia simplex
		Herposiphonia tenella
		Laurencia poitei

[1] Includes species recorded during the study on six or more occasions.

Species of tropical Caribbean affinity were possibly transported to the area by the Caribbean Current from Central America which flows into the Gulf of Mexico between Cuba and Yucatan. Pelagic *Sargassum fluitans* and *S. natans* were washed onto the shore and were often heavily epiphytized by benthic marine algae. Thus the *Sargassum* epiflora may possibly constitute a source of tropical "seed material."

Certain of the species reported only for the southwest jetty are of cool temperate North Atlantic affinity, e.g., *Porphyra leucosticta*, and are probably relicts from the Pleistocene (see section on disjunct distribution).

The algae may have been present in the bays during the study but in minute quantities and were thus overlooked. Many species are probably present as inconspicuous germlings, basal parts, or alternate phases and become conspicuous only when conditions are favourable. This was certainly the case with many annuals, e.g., *Ectocarpus siliculosus* and *Petalonia fascia*, which appeared each year when conditions were favorable but which could not be found at other times of the year.

Vertical Distribution

The universal arrangement of benthic marine algae into vertical zones is one of the most distinctive features of the shore (Stephenson and Stephenson, 1949). The occurrence of the algae in zones on the jetties at Port Aransas was reported first by Whitten, Rosene and Hedgpeth (1950) and Hedgpeth (1953). Zonation was apparent during the present study on vertical faces such as pier posts, sea walls, and bridge supports in Aransas and Redfish Bays, but was most evident on the southwest jetty at Port Aransas, where the three major zones could be readily discerned. The tidal range was small (Fig. 3), and since the jetty extended out into the sea, wave action became a major factor in effecting vertical water movements. The wave action increased with distance along the jetty so that towards the seaward end the algal zones were wider and raised relative to those on the landward end of the jetty (Hedgpeth, 1953). The raising of the zones in response to increasing wave action was similarly observed by Burrows, Conway, Lodge and Powell (1954) on Fair Isle, Scotland. The algae extended higher up the jetty on the south than on the north side in summer since the prevailing southeast winds increased the wave action on the former relative to the latter side. During winter when "northers" occurred, differences between the vertical extent of the zones on the two sides of the jetty were minimized. Seasonal changes in sea level take place in the Gulf of Mexico which are greater than the average daily change; the highest average monthly values occur in March-April and in September-October (Marmer, 1954). The algal zones are dynamic and migrate upwards during periods of wetting and downwards during prolonged exposure to the atmosphere due to desiccation, exceptionally high or low temperatures, or heavy rain. An alternating recolonization and retreat of algae on the shore were described similarly by Williams (1948) in North Carolina and Humm & Caylor (1957) in Mississippi. Seasonal variations in the tidal factor also had a pronounced effect on intertidal vegetation in Ghana (Lawson, 1957). India (Umamaheswararao and Sreeramulu, 1964) and in Trinidad (Richardson, 1969). The vertical

distribution of benthic marine algae in the above localities is thus dynamic and cannot be correlated directly to tidal levels.

The vertical extent of the vegetation towards the seaward end of the southwest jetty, Port Aransas was estimated visually to be approximately 3 M in summer, with the algae extending 1 M above and 2 M below Mean Sea Level. However the vertical range of the zones was often considerably less. The dominant algae in the littoral fringe were *Enteromorpha clathrata* and *Chaetomorpha linum*, in the eulittoral zone. *Ulva fasciata*, *Gelidium crinale*, *Centroceras clavulatum* and *Bryocladia cuspidata*, and in the sublittoral zone *Padina vickersiae*, *Agardhiella tenera* and *Rhodymenia pseudopalmata*. During the winter and early spring, the vertical range of the vegetation was reduced, since the sublittoral algae, which are predominantly of tropical Caribbean affinity, disappeared or persisted in reduced stature and were not replaced by species of cool temperate North Atlantic affinity. *Bangia fuscopurpurea* dominated the littoral fringe and *Petalonia fascia* and *Porphyra leucosticta* the eulittoral zone during the cooler part of the year. The vertical extent of the zones was thus extremely limited and similar to that at Beaufort, North Carolina where Hoyt (1920) recorded a total range of 2.2 M. Hoyt attributed the small range to the turbidity of the water, which greatly diminished the penetration of light; he recorded algae from a depth of 25.5 M on a reef where the water was clearer. Phillips and Springer (1960), Taylor (1961) and Williams (1951) similarly recorded algae at great depths in clear water. However in hot climates like Texas, algae from parts of the shore which are exposed to the air by water movements may be affected by elevated air temperatures and by desiccation, and their growth may be curtailed, which thus also limits the vertical extent of the shore.

Seasonal Distribution

The pronounced seasonal change in the growth of the algal vegetation of the region was a distinctive feature of the local flora and is characteristic of the warm temperate flora of the mid-Atlantic North American coast from Cape Cod to Cape Kennedy (Edwards, 1969b). The flora may be divided into three groups based on the season of maximum growth: species that grew throughout the year, and those that thrived either during the summer and autumn or during the winter and early spring, and declined in growth markedly or even disappeared during the unfavorable (for them) part of the year (Table 5). Species which demonstrated good growth throughout the year or in the warmer months were largely of tropical Caribbean affinity, while those that appeared in winter and early spring were mainly of cool temperate North Atlantic affinity. Edwards (1969b) cultured twelve red and brown algae from the Port Aransas, Texas area in an attempt to elucidate the causal factors of the distinctive seasonal alteration of the benthic marine algal flora of that region. The results supported the widely held view that temperature is of primary importance, but seasonal variations in daylength, acting alone or in conjunction with temperature variations were also implicated. Seasonal variations in light intensity did not appear to be involved. However, in Britain seasonal changes in total light energy appeared to control the develop-

ment of young stages in the sublittoral brown algae *Laminaria digitata, L. hyperborea* and *L. saccharina* (Kain, 1966), *Saccorhiza polyschides* (Kain, 1966; Norton and Burrows, 1969), and *Desmarestia aculeata* (Chapman and Burrows, 1970).

Species that demonstrated maximum growth during one part of the year often apparently disappeared during the remainder of the year, e.g., *Petalonia fascia, Bangia fuscopurpurea* and *Porphyra leucosticta.* Many of the species which did not possess a heteromorphic life history but which apparently disappeared at certain times of the year probably persisted as viable but inconspicuous plant holdfasts or bases. Dixon (1965) described how *Ceramium* died back to a few-celled perennating fragment which regenerated during the spring in Britain. Several red algae in Redfish Bay, e.g., *Digenia simplex* were observed to regenerate new branch systems in the spring, as reported by Conover (1964).

Those species that produced approximately equal numbers of sexual and sporophytic individuals in nature probably possessed a typical diplobiontic life history, e.g., *Gracilaria foliifera, Callithamnion byssoides* and *Polysiphonia denudata.* The latter two were shown to possess this type of life history in culture (Edwards, 1969a, 1970). Several species were observed to produce only tetrasporangia during the study, e.g., *Hypnea cornuta* and *Ceramium fastigiatum f. flaccida,* so that the life history of these algae may deviate from the "theoretical life history," as Dixon (1965) indicated may occur for certain species in Britain. The sexual phase may possibly be absent and the life history consist of a sequence of tetrasporic phases as Sundene (1962) demonstrated in culture for certain strains of *Antithamnion boreale* and West (1970) for *Rhodochorton concrescens.* Several species were collected in a vegetative state throughout the study, e.g., *Polysiphonia tepida, Digenia simplex,* and *Laurencia poitei,* and many of the dominant algae in the bays were rarely in fruit. Since *Grateloupia filicina* and *Hypnea musciformis* fruited on the southwest jetty, Port Aransas but not in the bays, the latter environments were possibly inimical to fruiting. The environmental tolerances for growth are possibly less stringent than for reproduction in these two species, and the populations in the bays may have been derived from the spores of the jetty populations.

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THE EFFECT OF TEMPERATURE AND SWIMMING SPEED ON THE OXYGEN CONSUMPTION OF TWO SNAPPERS, *LUTJANUS CAMPECHANUS* (POEY) AND *RHOMBOPLITES AURORUBENS* (CUVIER)

Richard H. Moore

University of Texas, Marine Science Institute, Port Aransas, Texas 78373

ABSTRACT

Respiratory rates and swimming speeds of red snapper, *Lutjanus campechanus* (Poey), and vermilion snapper, *Rhomboplites aurorubens* (Cuvier), were determined at 12.5°, 18°, and 27.5° C. The relationship of oxygen consumption to temperature is similar to that found in other fish species with values at 18° of 112 and 70 mg/kg/hr for red and vermilion snapper, respectively. Maximum sustained swimming speed and "scope for activity" show similar relationships to temperature for each species; however, the differences in "scope" between the two species probably have zoogeographical and ecological importance. The cold-lethal temperature of vermilion snapper is estimated to be not far below 12.5° during the spring months. For red snapper the cold-lethal temperature is undoubtably somewhat lower.

INTRODUCTION

The red snapper *Lutjanus campechanus* (Poey) and the vermilion snapper *Rhomboplites aurorubens* (Cuvier) are two fish species belonging to the family Lutjanidae, which can be collected off the Texas coast. Both species are commonly caught from the "snapper banks", a series of offshore reefs in the northwestern Gulf of Mexico at a depth of about 15 meters.

Moseley (1966a) has described the general biology and life history of the red snapper (as *L. aya* (Bloch)), and also (1966b) summarizes what little is known of the biology of the vermilion snapper. Apparently red snapper schools frequent the steep slopes of the snapper banks while vermilion snapper schools swim more freely over the upper slopes and tops of the banks.

The Lutjanidae are primarily distributed in tropical marine waters about the world, although some species venture into cooler temperate waters or brackish estuaries and mangrove swamps, and a number of genera are found only in water deeper than 200 meters. Since these fish live near the bottom in fairly deep water, they are found in an environment which does not experience the more drastic climatic fluctuations of more inshore waters. The habitat in which a majority of the lutjanids are found leads to the conclusion that most are relatively stenothermal, stenohaline marine species.

This study was conducted to investigate the effect of temperature and swimming speed on oxygen consumption rates and the effect of temperature on sustained swimming speeds for the two species.

The majority of studies on fish respiration have been conducted on temperate species (Winberg, 1956; Brett, 1970), a few studies concern arctic and antarctic stenothermal species, but very little work has been done with tropical marine fish (see Table 3 for references).

MATERIALS AND METHODS

Fish were collected by hook-and-line from the Eastern and Aransas Reefs off Port Aransas, Texas (for locations see Moseley, 1966b), on 2–3 March, 1972. Surface water temperature at this time was 19°C. Bottom temperature was not measured, however, Moseley (1965) recorded bottom temperatures on the snapper banks during March only 1°C lower than surface temperatures. Due to the depth at which these fish live only a few of the fish caught could be brought back to the laboratory alive and in good condition. It was noted that vermilion snapper appeared to survive the ascent better than did red snapper, most of which, even when the swimbladder was not everted, experienced difficulty in swimming and maintaining themselves in an upright position. Only apparently healthy fish were used in experiments.

In the laboratory the fish were maintained in a temperature controlled marine aquarium equipped with a gravel filtration system and recirculating, aerated water. The fish were held on natural photoperiods at 18–19°C for one week and were fed every two days on small fish. Both species were observed feeding and there was no mortality during this period.

Oxygen consumption experiments were conducted at 18°, 12.5°, and 27.5°C. These temperatures correspond to the surface temperature at the collection sites and the upper and lower temperatures at which red snapper have been collected (Rivas, 1970). Fish were acclimated to each of these experimental temperatures for two days during which time they were not fed. Following each set of experiments the fish were fed and acclimated to another temperature. Oxygen consumption and swimming speeds were measured simultaneously on six fish of each species at each of the acclimation temperatures. When additional fish were available additional swimming speed experiments were conducted. The experimental procedure and design of the rotating respiration chambers have been described by Wohlschlag (1957).

Since, during a particular experiment the rotation speed of the chambers could be varied, fish were allowed to swim at whatever speed they chose or were forced to swim as rapidly as they were able during the 10 or 15 minute period between water samples (sustained swimming). Fish which did not swim steadily were allowed to rest, the chamber being rotated only during the last minute in order to mix the water in the chamber. Resting fish remained more or less motionless in the chamber. Any fish which showed restlessness was allowed to swim at a slow speed or rest, as it desired. The revolutions of the chamber were counted by means of a counter attached to the rotating shaft and any revolutions gained or lost by the fish were considered in the final calculation of the total distance swum.

Analysis of the data was done on the University of Texas C.D.C. 6400/6600 computer system.

Data on three biological functions were obtained: oxygen consumption, sustained swimming speed, and mortality at each of the three acclimation temperatures.

Oxygen consumption was related to log weight, temperature, and swimming speeds by multiple regression equations of the form:

$$Y = a + b_w X_w + b_t X_t + b_s X_s$$

where:

Y = the log of the expected value of oxygen consumption (mg O_2/hr)

a = the y-intercept (a constant)

b_w, b_t, b_s = partial regression coefficients respectively for log weight temperature, and swimming speed; eg. b_t represents the change in Y per unit change in X_t with the other variables held constant.

X_w, X_t, X_s = the log weight (gms), temperature (°C), and swimming speed (standard lengths/second), respectively.

m = number of fish tested

Swimming speeds were expressed in SL/sec rather than in terms of actual distance swum

(m/min) since it is felt that this measurement reduces possible differences in distance covered due to the different sizes of the fish (Brett, 1964).

Following calculation of regression equations variables not contributing significantly (P less than 0.05) to the regression were deleted and the equation recalculated. For vermilion snapper all three variables were significant; for the red snapper, however, weight was not, probably due to the narrow range of weights available.

RESULTS

Table 1 gives the data used in the calculation; the final multiple regression equations are given below and the statistics for these are given in Table 2.

for vermilion snapper (m = 16)

$$Y = -1.60346 + 1.2102\,X_w + 0.0214\,X_t + 0.0851\,X_s$$

for red snapper (m = 18)

$$Y = 1.39007 + 0.0216\,X_t + 0.0793\,X_s.$$

Graphs relating sustained swimming speed to temperature are given in Figure 1.

TABLE 1

Oxygen consumption and swimming speed data used in calculating multiple regression equations

Species	Fish number	Weight gms	Acclimation temperatures 12.5° mgO_2/hr	12.5° SL/sec	18° mgO_2/hr	18° SL/sec	27.5° mgO_2/hr	27.5° SL/sec
Vermilion snapper	1	398	74	0.61	..	...	170	1.81
	2	305	69	0.64	68	1.57	(2) 118	0.67
	3*	255	..	...	72	1.50	131	1.42
	4**	350	69	0.31	80	0.07	105	0.07
	5	240	33	0.83	66	1.09	(5) 120	1.70
	6*	330	11	0.04	71	0.92	63	0.08
	7*	340	..	...	69	0.57	..	...
Red snapper	1	450	38	0.32	91	0.92	115	0.78
	2*	448	..	...	50	0.05	(3) 115	1.34
	3	378	22	0.36	75	1.15	84	1.09
	4	289	47	0.37	84	2.05	115	1.89
	5	284	36	0.14	73	0.03	(5) 105	1.08
	6**	308	25	0.30	..	...	83	0.75
	7	324	29	0.32	91	0.83	57	0.32

* = died at 12.5° ** = died at 27.5°
Bracketed figures indicate multiple experiments on a single fish.

TABLE 2

Statistics for multiple regression equations

Equation	Degrees of freedom	Multiple correlation R	P	Standard deviation of estimate	Standard errors and probabilities of partial regression coefficients ^sb_w	p	^sb_t	p	$^sb_{ss}$	p
Vermilion snapper	14	0.860	**	0.0718	0.2688	**	0.0033	**	0.0344	*
Red snapper	16	0.840	**	0.0741	.....	(NS)	0.0036	**	0.0369	*

Probabilities: NS = not significant; * = 0.01 p 0.05; ** = p 0.01
..... = term not included in final equation.

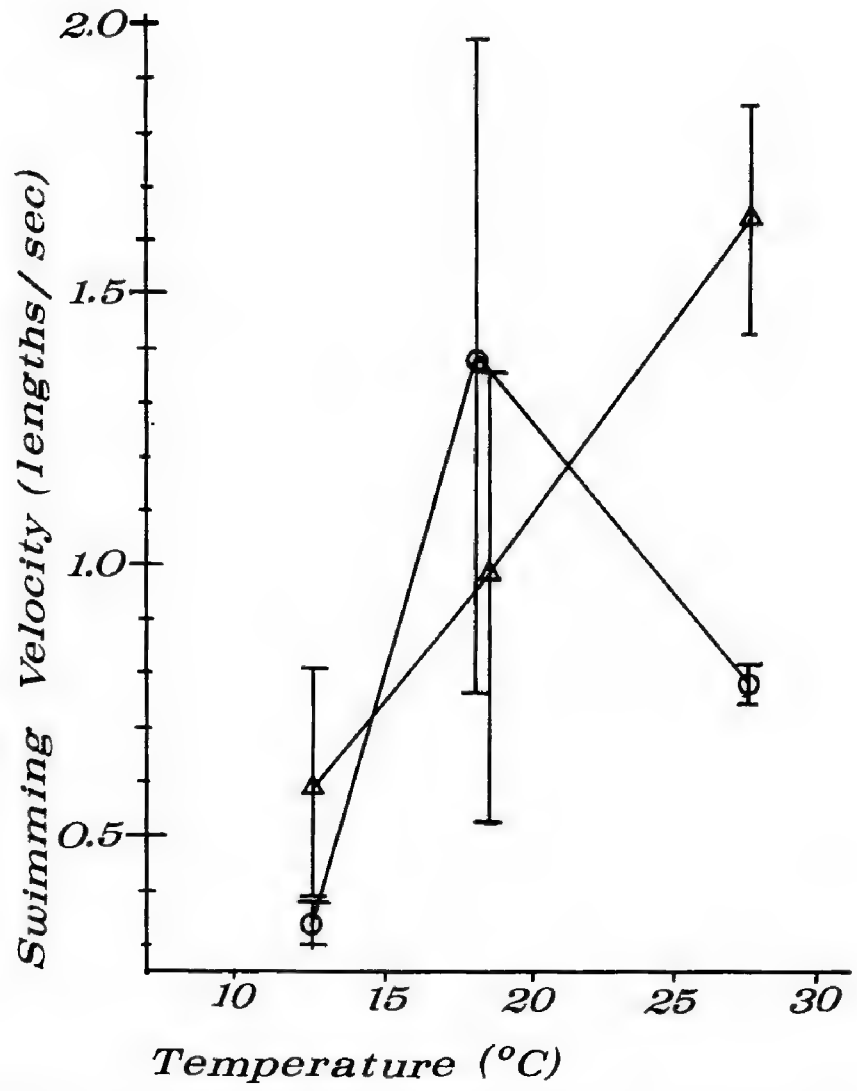

FIG. 1. Relationship between temperature and maximum sustained swimming speed for vermilion and red snapper. Circles (red snapper) and triangles (vermilion snapper) indicate means, vertical lines indicate one standard deviation above and below the mean.

DISCUSSION

The two species of snapper considered here exhibit oxygen consumption rates comparable with those of other subtropical and tropical marine species.

The partial regression coefficients for temperature are well within the range of coefficients reported for other species of fish (Winberg, 1956; Brett, 1970). The weight coefficient for vermilion snapper is higher than the 0.8 value commonly regarded as typical for fishes (Winberg, 1956; Brett, 1970). Such high values are however quite commonly found when active rather than standard metabolic rates are measured (Brett, 1964; Beamish, 1970). Scholander, Flagg. Walters and Irving (1953) have reported coefficients as high as 0.94 for some tropical marine fishes. Since these experiments were conducted on active swimming tropical fishes the high weight coefficient was not unexpected.

Less is known of the relationships between swimming speed coefficients and physiological-ecological requirements of fish than is known for temperature or weight coefficients. It is well documented that activity increases oxygen consumption (Brett, 1970), however, the differences in the magnitude or rate of these increases found in different species have not been adequately reviewed, although the metabolism-swimming speed regressions tend to be linear within the limits of swimming speed, size, and experimental variables (Tytler, 1969;

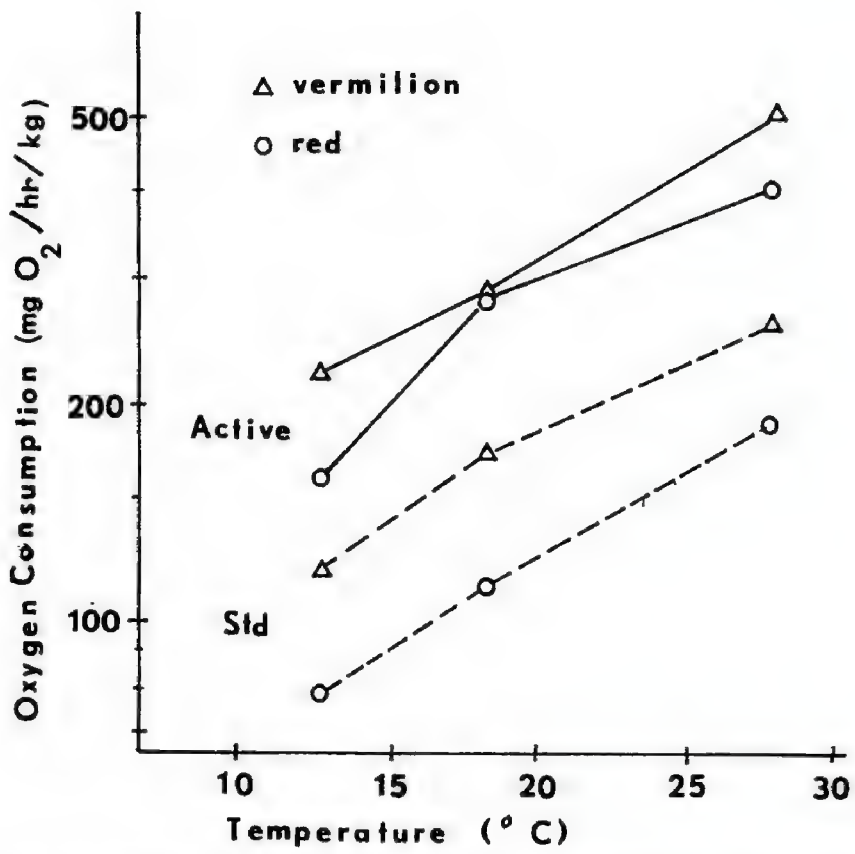

FIG. 2. Comparison of active and standard oxygen consumption rates for vermilion and red snapper at each of the three acclimation temperatures. (Circles = red snapper, triangles = vermilion snapper, solid lines = active metabolism, dashed lines = resting metabolism).

Brett, 1964, 1970). Much of the difficulty in comparing data given for different species stems from the different ways in which various authors have presented their data.

Figure 2 shows the observed oxygen consumption for the two species at different activity levels. Oxygen consumption is expressed as mg. oxygen consumed per hour per kg for an average sized fish (300 g.) in both active (highest observed swimming speed) and standard (extrapolated from lowest observed swimming speed) metabolic states.

"Scope for Activity" or the metabolic cost of swimming is given by the difference between the standard and active metabolic rates. Fry (1947), Brett (1971), and others have shown that maximum "scope" and maximum swimming velocities are usually associated with preferential or optimum temperatures and that interspecific differences often reflect ecological requirements of the animals. If "scope" is plotted against temperature (Fig. 3) an interesting pattern develops. Red snapper have a maximum "scope" at the intermediate temperature while vermilion snapper have their maximum "scope" at the highest experimental temperature, exactly the same pattern which was seen in the relationship between swimming speed and temperature for the two species.

The differences in optimum temperature for swimming and "scope" are related to the distributions of these species. *Lutjanus campechanus* is found farther north than other snappers, occurring regularly north of Cape Fear, N. C. (Rivas, 1970), while *Rhomboplites aurorubens* occurs only as far north as the South Carolina coast (Jordan & Evermann, 1898). Although the vermilion snapper is usually considered a more offshore species than the red snapper (Bohlke & Chap-

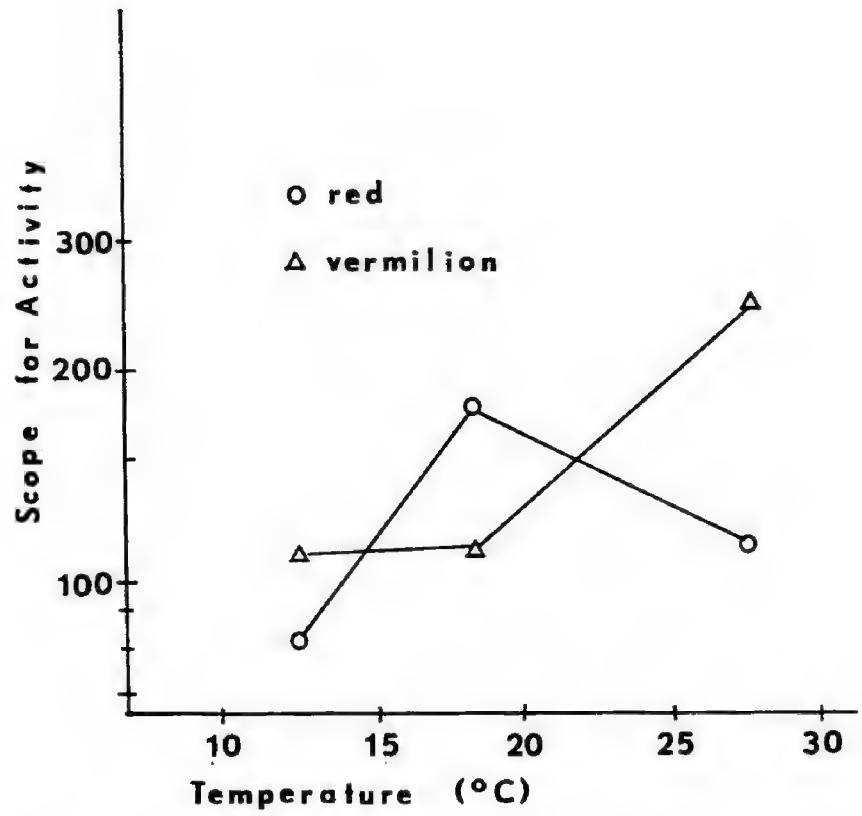

FIG. 3. Relationship of "Scope of Activity" and temperature for vermilion (triangles) and red snapper (circles). "Scope" = Active—Standard Metabolism (mg O_2/kg/hr).

lin, 1968) most commercial snapper fishermen feel that where the two species occur together the vermilion snapper will be found nearer the surface, and so in presumably warmer water. The relationships of swimming speed and "scope" with temperature may therefore have zoogeographical significance, reflecting the differences in latitudinal and bathymetric distribution of the two species.

Comparison of the metabolic rates from this study and published data on other subtropical marine species shows considerable variation, as in Table 3. Certainly part of this variation can be attributed to differences in technique and sizes of animals used as well as to inherent differences between the species. For example, the snapper, *Lutjanus apodus*, used by Scholander *et al.* (1953) all weighed less

TABLE 3

Comparison of standard metabolism with other tropical and subtropical marine fishes

Species	Temperature and standard oxygen consumption (mgO_2/hr/kg)			Source
Lutjanus campechanus	12.5°, 80	18°, 112	27.5°, 187	1
Rhomboplites aurorubens	12.5°, 114	18°, 170	27.5°, 259	1
Lutjanus apodus	15°, 185	20°, 314	30°, 857	2
Haemulon bonariense	15°, . . .	20°, 199	30°, 571	2
Scarus croicensis	15°, . . .	20°, 285	30°, 571	2
Cynoglossus brevis	15°, 60	20°, 100	30°, 240	3,4
Cynoglossus puncticeps	15°, 46	20°, 63	30°, 145	4
Halophryne dussumeri	15°, 21	20°, 32	30°, 83	3
Lagodon rhomboides	10.8°, 42	20°, 114	25°, 257	5

SOURCES: 1) this study; 2) Scholander et al., 1953; 3) Edwards et al., 1970; 4) Edwards et al., 1971; 5) Wohlschlag et al., 1968.

than 3 grams, and small fish have a higher oxygen consumption per unit of body weight than do large fish (as shown by the weight coefficient). The flatfish studied by Edwards *et al.* (1971) and the toadfish (Edwards *et al.*, 1970) are benthic fishes which as a group have a low metabolic rate (Moore & Wohlschlag, 1971). The rates for both species of snapper presented here and for the subtropical pinfish *Lagodon rhomboides* (Wohlschlag *et al.*, 1968) fall between the "high" values of Scholander *et al.* (1953) and the "low" values of Edwards, Baxter. Gopalan, Mathew and Finlayson (1971). Wohlschlag (1964, figure 8, page 58) illustrates that polar and cold adapted temperate fishes at temperatures of 0°C, or slightly above, have metabolic rates which cover a wider range than do the rates of warm temperate or tropical species. The inclusion of the data of Edwards *et al.* (1971) and this study into Wohlschlag's (1964) figure reduces the lower limit of respiration for tropical fishes to values comparable with those of "cold adapted" polar fishes.

What results is a more or less similar metabolic rate in similar fishes from all latitudes. "Cold adaptation" is a genetically acquired means for maintaining higher metabolic rates at cold temperatures and a similar phenomenon, "warm adaptation", may reduce metabolic rates in tropical fishes at higher temperatures. One may ask what advantage it is to the organism to maintain a metabolic rate at a level lower than that which environmental temperatures would sustain? Edwards *et al.* (1971) suggest two possibilities: one, that metabolic rates are limited in the tropics not by temperature but by dissolved oxygen levels, and two, that lower metabolic rates are the result of energy conservation due to a greater amount of competition for food resources in the tropics. More experimental work will be needed before either, or both, of these hypotheses can be evaluated.

Rivas (1970) states that the temperature limits at which *L. campechanus* has been collected are 12.7° and 27.7°, however Moseley (1966a) found small snappers inshore at temperatures as high as 30°. Moseley (1966a) reports that off Texas red snapper are rarely caught at temperatures below 16°. No comparable information is available for *R. aurorubens* however the fact that more vermilion snapper (three) than red snapper (one) died at 12.5° supports the hypothesis that vermilion snapper are less cold-tolerant. All fish at 12.5° were sluggish, some approaching a moribund condition, and there behavior and appearance conforms with observations made on several other species of fish at temperatures near their respective cold-lethal level (Moore & Wohlschlag, unpubl. & 1971).

SUMMARY AND CONCLUSIONS

1. Respiratory rate and swimming speed of red snapper, *Lutjanus campechanus*, and vermilion snapper, *Rhomboplites aurorubens*, were measured at 12.5°, 18°, and 27.5°. These temperatures correspond approximately to the minimum temperature at which red snapper have been collected, the surface water temperature at the collection site, and the maximum recorded temperature at which red snapper have been collected.

2. The relationship of oxygen consumption to temperature is similar to that of other marine fish species. Comparison of this data with other published data

on tropical marine fishes indicates that tropical marine fish exhibit a broader range of metabolic rates than temperate fishes do.

3. The relationship of maximum swimming speed and "Scope for Activity" with temperature are the same for each species although there is considerable difference between the two species. It is suggested that this difference is related to zoogeographical and ecological differences between the two species.

4. More deaths occurred among vermilion snapper (3) at 12.5° than among red snapper (1). Observations made on surviving fish at this time suggest that this temperature is near the seasonal cold-lethal level for vermilion snapper. The fewer deaths of red snapper is attributed to their greater resistance to cold which is reflected in their distribution.

ACKNOWLEDGMENTS

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A TRAWL STUDY OF NEARSHORE FISHES AND INVERTEBRATES OF THE GEORGIA COAST[1]

H. Dickson Hoese

Department of Biology, University of Southwestern Louisiana, Lafayette 70501

ABSTRACT

A trawl study was conducted for a 12 month period in 1956–66 on the central Georgia inshore continental shelf and adjacent Doboy Sound. Hydrographic data showed the area to be relatively salty, apparently subject to major influence by the Altamaha River, winds, but rarely by longshore currents. Turbidity best delineated the water masses with clear oceanic water about 6 miles offshore, occasionally with intermediate waters. The distribution of many species of motile invertebrates and fishes correlated with either the water masses or sediment type which became coarser offshore. The inshore fauna, a warm temperate one, was characterized by *Stellifer lanceolatus* and *Penaeus setiferus*. Offshore the fauna became subtropical, characterized by *Diplectrum formosum* and *Hemipteronotus novacula*. A small cool temperate fauna invaded during winter.

The absence of large benthic plant communities excludes the large fauna associated with it. However, the turbidity limiting plant growth was associated with up to 8 times the biomass found in clearer offshore waters. There was no evidence gathered indicating any potential unexploited commercial fisheries.

INTRODUCTION

The Georgia coast has been one of the least researched of coastal states, especially the fishes and larger invertebrates. Although the U.S. Fish and Wildlife Service has collected off the southeastern United States for many years (Bullis and Thompson, 1965), relatively few stations have been off Georgia. Some of the early trawling has been done by Bears Bluff Laboratory off South Carolina (Taylor, 1956). Considerable data on the fishes of the East Florida coast, an area also relatively unexplored, was given by Anderson and Gehringer (1965).

The Georgia literature on motile fishes and invertebrates is composed of papers by Weymouth, Lindner, and Anderson (1933), Lindner and Anderson (1956), Frisbie (1967), and Anderson in (1970), on shrimp; Rickards (1966) on tarpon; Anderson (1968) on fishes; Dahlberg (1970a, b) on analomous fishes; Dahlberg and Heard (1970) on elasmobranchs; Dahlberg and Odum (1970) on species diversity; Jorgenson and Miller (1968) on morphometry; and Miller and Jorgenson (1969).

[1] This study was conducted at the University of Georgia Marine Institute, Sapelo Island, Georgia, with funds from the Sapelo Island Research Foundation and the National Science Foundation.

Description of Study Area

The Georgia coast is part of a large salt marsh system extending from South Carolina to northern Florida. Large expanses of salt marsh dominated by *Spartina alterniflora* are interrupted by relatively narrow and deep sounds. The marshes are separated from the Atlantic Ocean by sandy barrier islands which are frequently dissected by small tidal streams.

The area of study was one of these sounds (Doboy) and adjacent ocean waters on the central Georgia coast (Figs. 1 and 2). The work was conducted from August 1965 through August 1966. Doboy sound is about 10 km long and 1–2 km wide with depths from 2 to 15 m at mean low water, except for the shallow perimeter. The tidal range in the area averages a little over two meters with maximum extremes of 1.3 to 3.4 m. The list of stations and their characteristics is shown in Table 1.

METHODS

Collections were made almost exclusively with a 40 foot balloon shrimp trawl with a cod covered with a small mesh liner to capture small forms. The net was damaged in September so a 30 foot net with ¾ inch mesh was substituted during that month. Collections in the Duplin (Stations 7 and 8) were made with a small try net with 1½ inch mesh. The trawl was pulled for 10 minutes at stations 1, 2, and 3; 15 minutes at stations 7 and 8; and 20 minutes at stations 4 and 5. The large net was pulled at a constant engine rpm (7500) by the research vessel Kit Jones. The ocean stations were usually completed in one day, with the sound stations on an adjacent day. Data from the Duplin stations is included only where it clarifies the life history of species taken at the regular stations, and counts are usually based on catches at stations 1–5. All samples were preserved at 10% formalin, washed for several hours at the laboratory, then weighed and fifty of each of the common species measured. In some of the large catches only a fraction (over 20%) was counted and weighed and the remainder weighed together. Stations 4H and 10H were sampled for 10 minutes each month beginning in September to show inshore-offshore differences.

Salinities and temperatures were measured with an Industrial Instruments Induction Salinometer, model RS5–3, turbidity with a Hydroproducts Model 410 BR transmissometer with a model 411 sensor, which has a 10 cm light path, and oxygen with a YSI Model 51 meter.

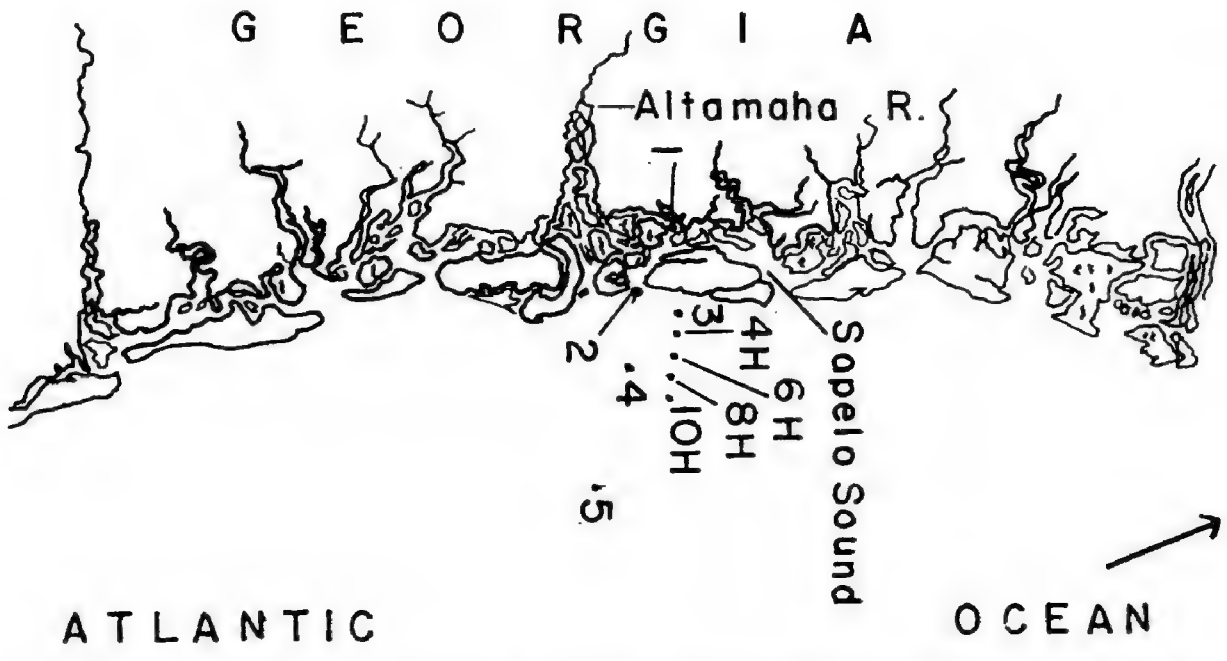

FIG. 1. Map of Georgia Coast, showing area studied and station locations.

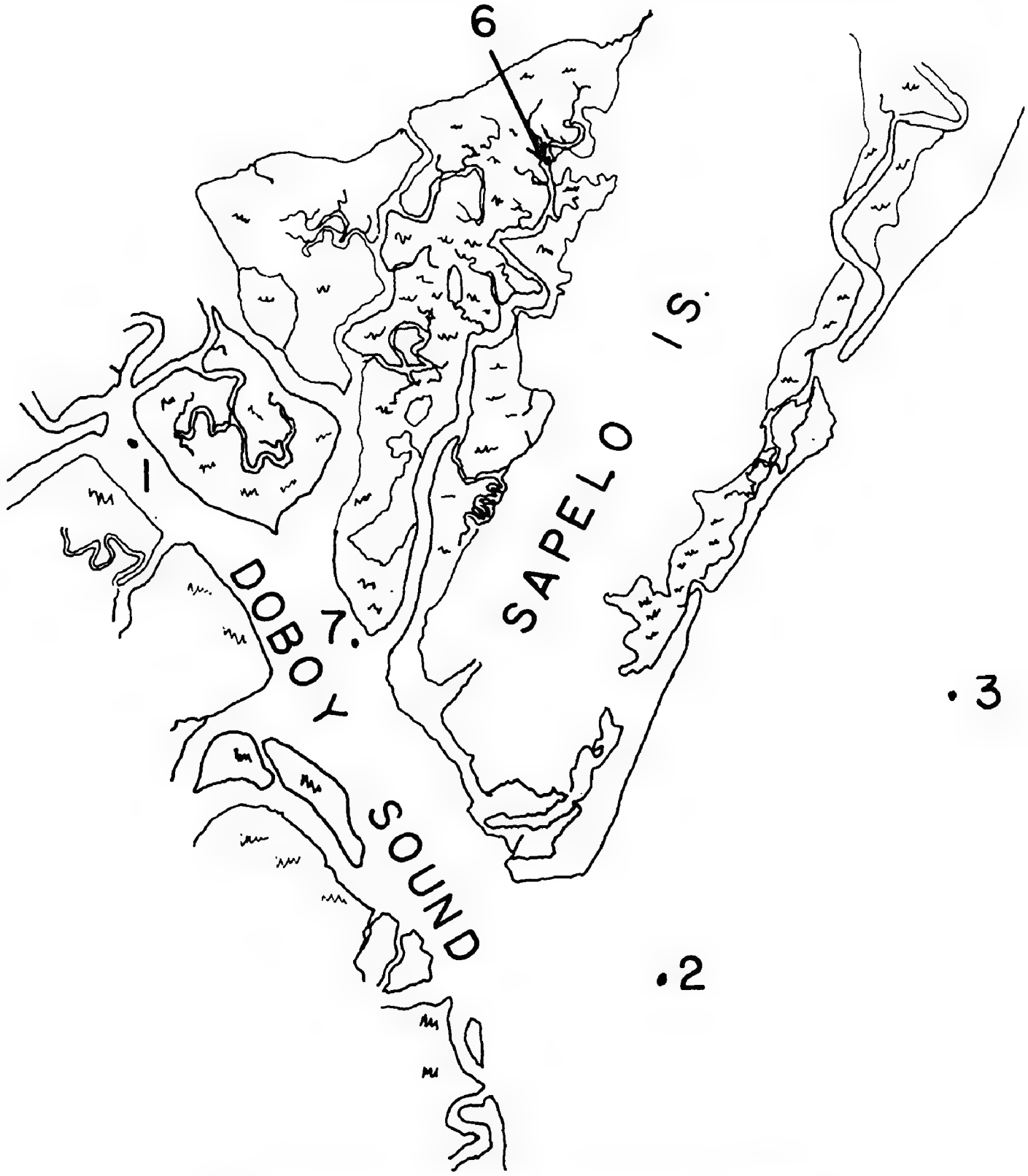

FIG. 2. Map of Doboy Sound showing inshore stations.

Lengths of bony fishes are standard lengths, squids are mantle, shrimp are rostrum-telson, crabs are carapace width, and others are total length.

HYDROGRAPHY

There is very little prior data on the inshore hydrography of the Georgia coast. Drake (1891) gave specific gravity readings taken during an oyster survey and found the highest readings in St. Andrews, St. Catherines and Sapelo Sounds. Galtsoff and Luce (1930) also surveyed Georgia oyster beds giving salinities for the whole coast. They found Sapelo to be the saltiest sound. The U.S. Fish and

TABLE 1

Description of Stations

Station Number	Location	Latitude	Longitude	Depth (M)	Bottom
1	Upper Doboy Sound	31°26.5′N	81°20.4′W	4–6.4	Mud with coarse Pleistocene sand in SE corner
2	Mouth Doboy Sound	31°22.2′N	81°15.4′W	6.4–9.8	Muddy fine sand
3	Off Cabretta Is.	31°24.3′N	81°13.3′W	4.3	Fine sand
4	About 7 miles off Doboy Mouth	31°19.4′N	81°09.2′W	9–11	Coarse and fine sand with irregular bottom
5	About 18 miles off Doboy Mouth	31°13.6′N	80°55.5′W	16.8	Mostly coarse sand
10H	10 miles off Cabretta Island	31°19.3′N	81°05.1′W	11.6	Coarse and fine sand with shell fragments
8H	8 miles off Cabretta Island	31°21.4′N	81°06.8′W	10.7	Coarse and fine sand with shell fragments
6H	6 miles off Cabretta Island	31°22.5′N	81°08.8′W	10.4	Fine sand
4H	4 miles off Cabretta Island	31°23.1′N	81°10.9′W	7.3	Fine sand
6	Doboy Sound at Mouth Duplin River	31°25.0′N	81°18.2′W	0.5–1.5	Mud
7	Upper Duplin	31°28.8′N	81°16.4′W	5–6.4	Mud

Wildlife Service has published extensive but largely unanalyzed hydrographic data from the 9 Gill cruises of the Southeast U.S. continental shelf in several Special Scientific Reports (latest summaries by Anderson, Gehringer and Cohen, 1956a and 1956b; Anderson, Moore and Gordy, 1961). However, there were few inshore stations in Georgia. Although the southeast U.S. coast offers an unusual set of unstudied conditions, little hydrographic work has been done. The present study was not designed to be hydrographic, but since some data of interest were obtained all the data were analyzed.

Although the inshore salt marsh system seems to be dominated by tides (Ragotzkie and Bryan, 1955), there seems to be a seasonal cycle in water density (sigma-t) (Fig. 3). This cycle appears to be largely independent of the tide at a given station, although a sequence of transects run in the summer shows strong stratification during the peak of flood tide lessening through peak ebb but strengthening again as the tide turned.

In September, at the beginning of the study the waters were stratified with the typical case of lighter water landward and upward. In October through December the waters became almost homogeneous except close inshore. Destruction of stratification was possibly due to both strong winter winds and cooling of surface waters.

In January and February a peculiar situation developed where lighter water

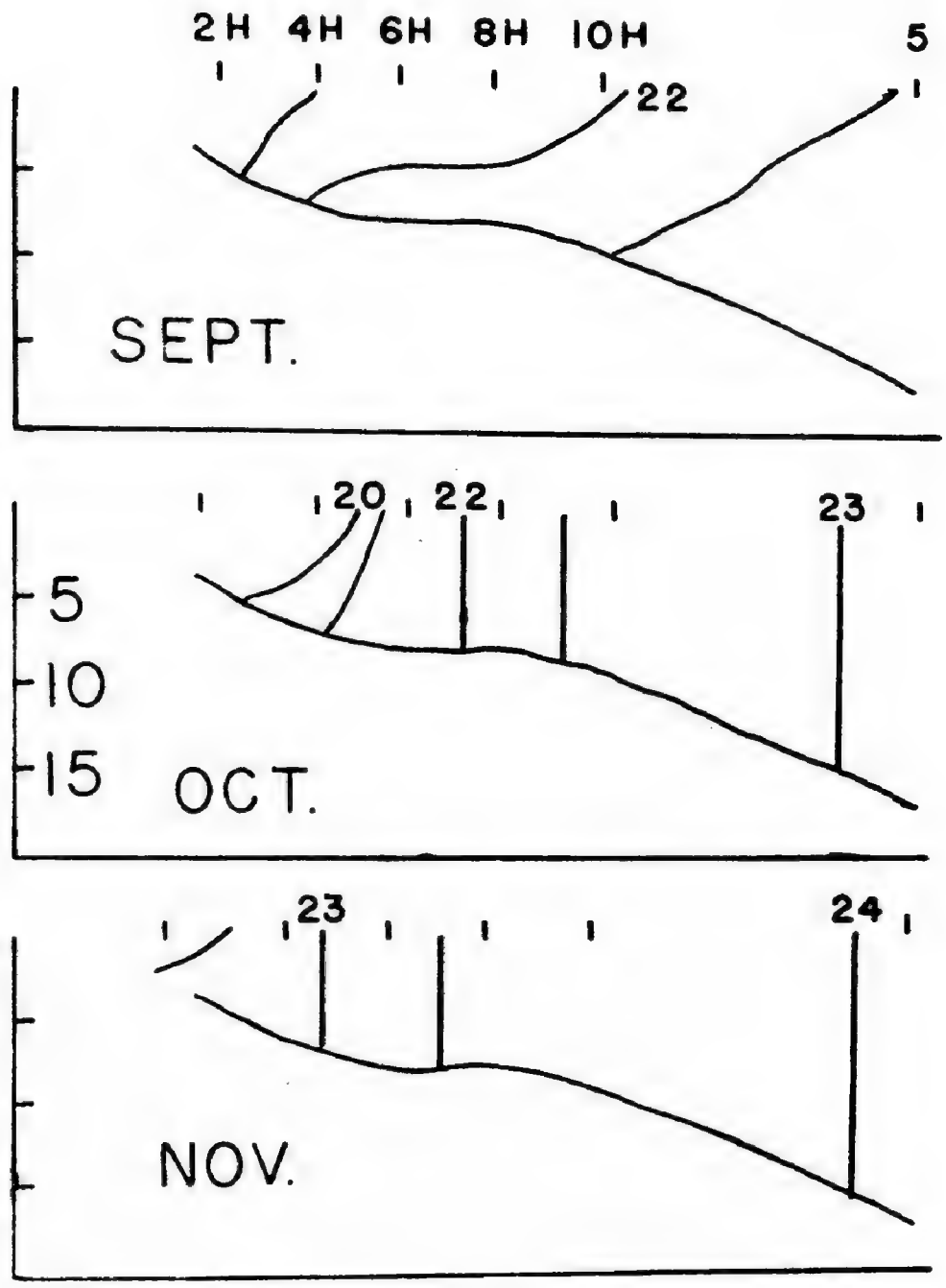

FIG. 3a

was either sandwiched between or lay under denser surface water. The condition is suggestive of longshore currents, but the causes are unknown. This may be consistent with the data of Bumpus and Lauzier (1965) which suggests strong southerly drift in winter. However, the evidence of Sargassum and turtle grass at station 5 in October indicates some fall northerly flow.

In March the waters became strongly stratified due to a large flood from the Altamaha River and surface warming. The strongest stratification was in the upper meter with very little below 5 m. In April the flood waters dissipated and what is apparently normal summer stratified surface returned. In May and June a smaller flood strongly stratified surface waters, but again in July and August there was a return to the small stratification of the previous September, thereby completing a cycle.

Salinity

When the study began in September there was a small amount of salinity

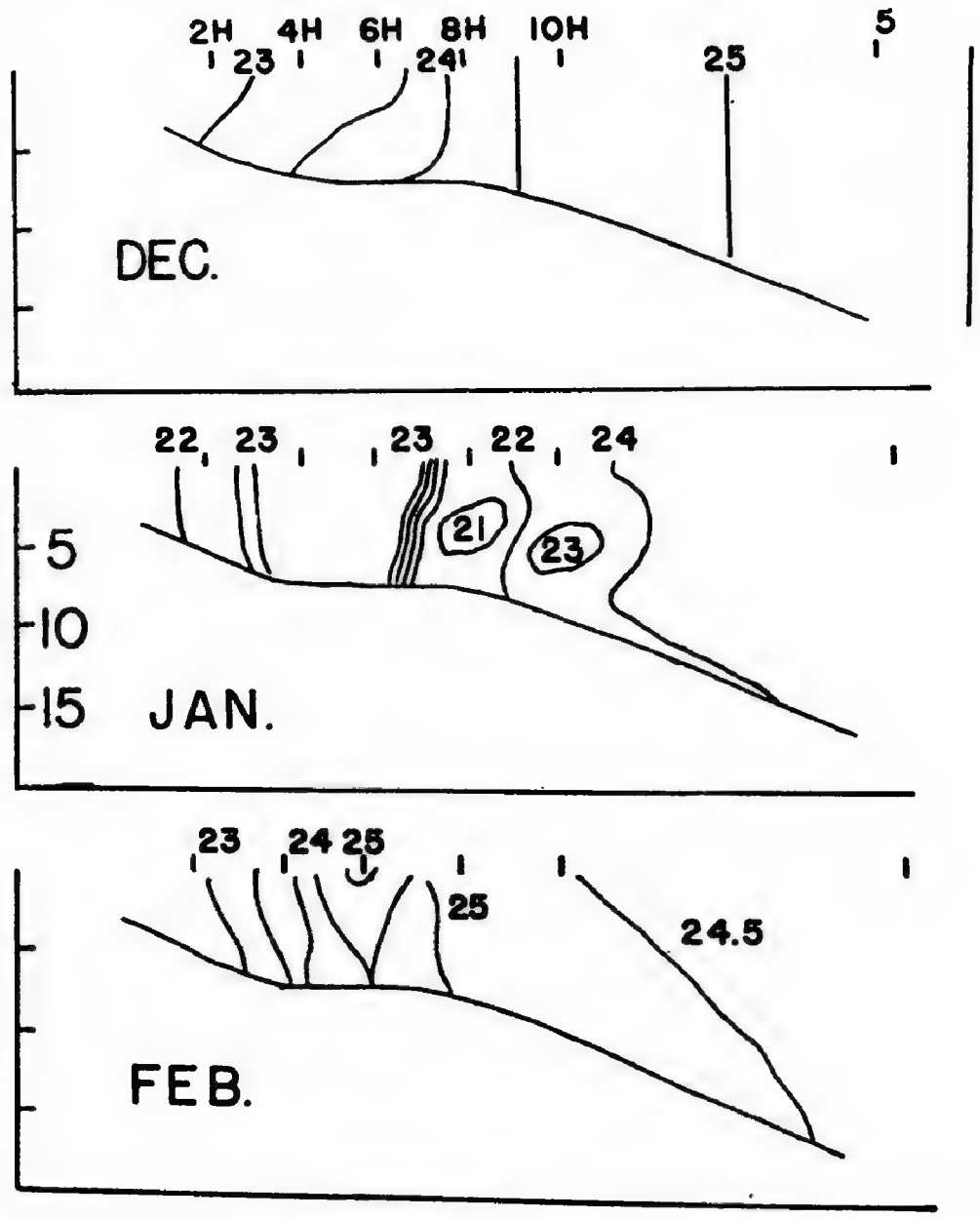

FIG. 3b

stratification at all stations ranging from 0.2–0.3 to sometimes over 1.5‰. This was a period of relatively calm winds.

In October through January during stronger winds most of the stations were unstratified, but stratification began again in February due to an influx of freshwater from the Altamaha River. During March, April and May the waters were strongly stratified, top and bottom salinities differing from 3 up to 7‰. In June only station 5 was unstratified and by July all stations were only slightly stratified, again beginning the pattern present at the start of the study.

It would seem that the tidal system in the study area is inadequate to cause total mixing under normal conditions of fresh water inflow, except when aided by strong, dense winter winds. During the large flood of the Altamaha River in March and the smaller one in May fresher water spread out over the denser sea water in a thin layer about a meter thick. During March river water could be traced as far as station 5 where the salinity was reduced to 21‰ from its normal range above 30‰. Surface salinities of the transect increased shoreward suggesting that the river water spread somewhat north only after it was several miles to sea. The remaining evidence of these floods a month later was only a slight lowering of normal salinities. Salinities over the area were relatively high even in the

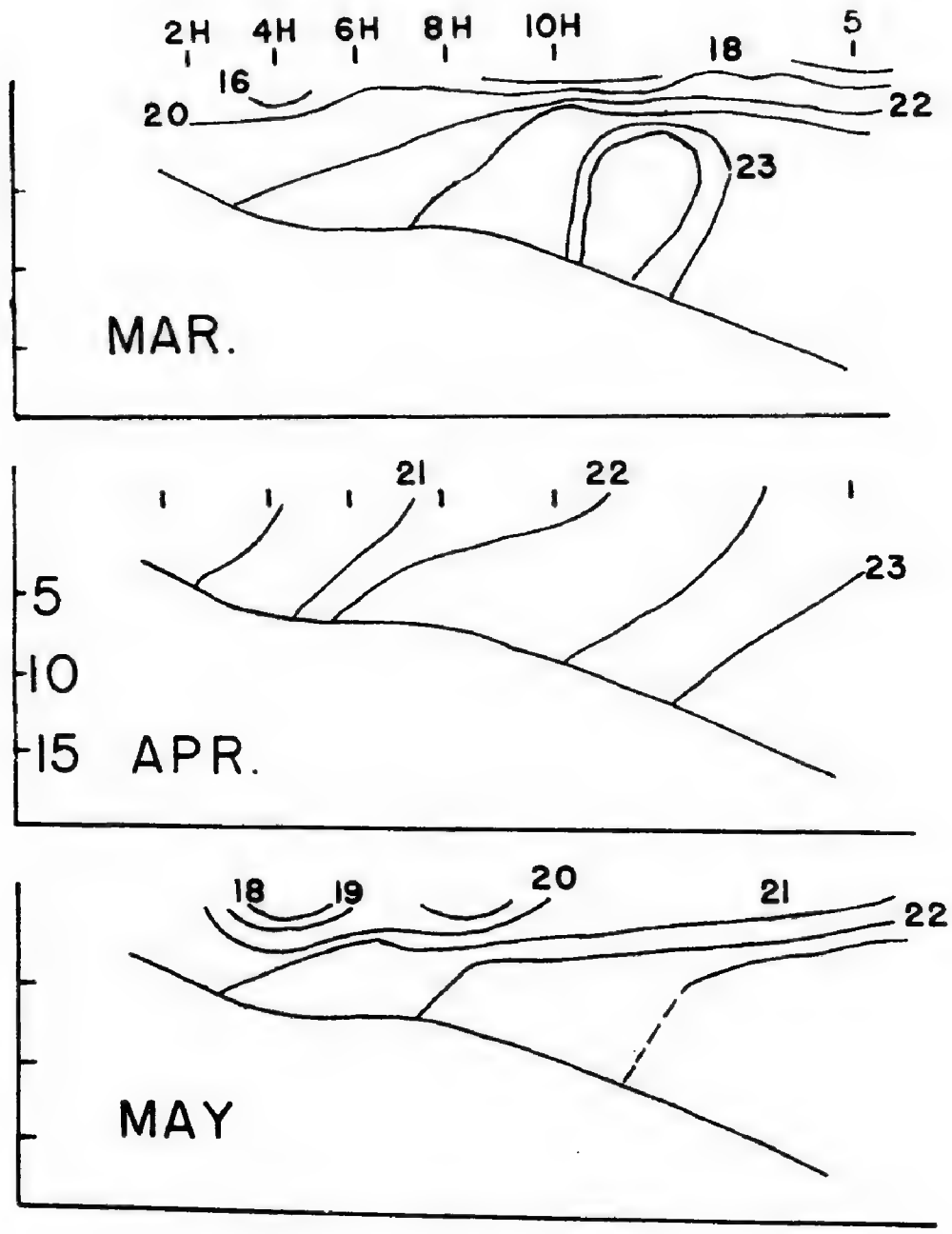

FIG. 3c

sounds, except during the spring floods when station 1 went to 7.2‰ on the bottom. Salinities in the sound were over 20‰ except for the brief floods of March and early June. The Duplin was somewhat fresher, the data previously published by Hoese (1967).

Temperature

The seasonal cycle of water temperature shows no unusual traits not present in previous data (Anderson, Moore and Gordy, 1961). Due probably to the depth of water, air temperatures are dissimilar and related only in general trends. Average temperatures varied from 12°C in February to 29°C in August (Table 2), typical of many warm temperate latitudes. December through February were consistently cold and June through September warm with moderately changing temperatures in other months.

Turbidity

The most striking feature of inshore Georgia waters is the high turbidity. Light

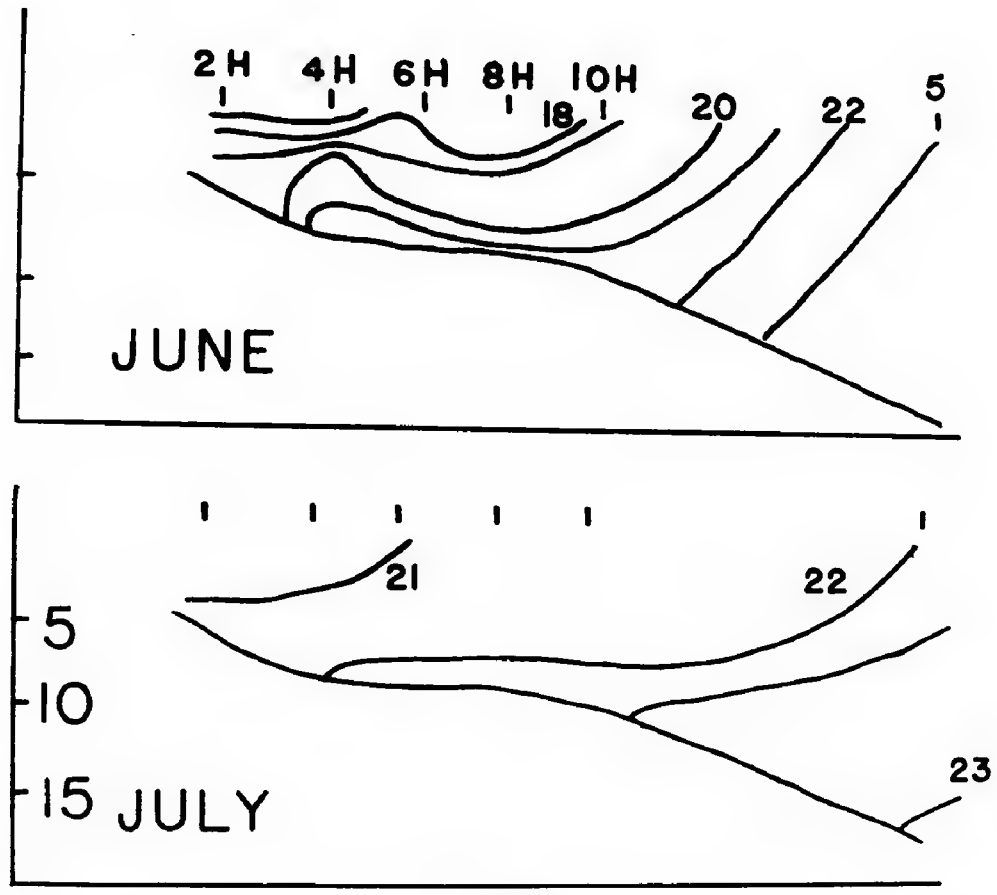

FIG. 3d

FIG. 3. Seasonal cycle in water density (sigma-t).

TABLE 2

Seasonal temperatures at main stations

		Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
5	S	28.2	27.1	23.9	19.4	15.9	14.5	10.9	17.3	20.1	23.8	26.0	28.4
	B	25.6	26.8	23.9	19.4	15.9	15.5	10.7	14.8	19.9	23.3	25.5	26.2
4	S	29.3	27.3	23.1	18.7	14.4	14.3	11.2	15.9	18.3	23.3	26.6	28.1
	B	28.0	27.1	23.2	18.7	14.4	15.0	10.3	13.6	17.3	22.2	25.3	27.4
3	S	29.4	27.9	23.1	17.9	12.5	12.4	. . .	17.5	19.8	22.9	27.1	28.7
	B	28.4	27.2	22.8	17.7	12.5	12.6	. . .	14.4	18.5	22.8	25.9	27.5
2	S	29.5	28.2	22.5	18.0	12.3	11.8	12.6	15.5	18.8	23.7	26.6	29.8
	B	28.6	28.0	22.4	18.1	12.3	11.8	12.6	15.7	17.3	25.3	25.9	28.6
1	S	30.1	27.2	24.3	16.5	12.4	12.3	13.6	16.6	18.6	23.8	27.4	30.1
	B	30.6	27.3	25.2	16.5	12.4	12.3	13.8	16.7	18.0	23.1	27.3	29.5
Avg.	S	29.3	27.5	23.4	18.1	13.5	13.1	12.1	16.6	19.1	23.5	26.7	29.0
	B	28.2	27.2	23.5	18.1	13.5	13.4	11.9	15.0	18.2	23.1	26.0	27.8

S = Surface
B = Bottom

penetrates only a slight distance (Ragotzkie, 1960), and productivity of the water column is believed to be low because of light limitations. Offshore the barrier islands the water clears, sometimes gradually and sometimes rapidly at convergence lines. Beyond ten miles, the water was nearly always clear. Readings here never went below 95%, and usually were near 100. Between 10 and 4 miles offshore, the water usually began to get turbid, becoming eventually the brown color of salt marsh water. This intermediate greenish water usually measured 80–90% light transmission, whereas the brown water ranged from 2 to 76. This band of turbid inshore water shows up clearly in three satellite photographs of the area (Nicks, 1970). These pictures show this band to be prominent at least from South Georgia to the Waccamaw River mouth, South Carolina. During the March flood offshore surface waters turned brown with river water, but readings were between 91 and 96. Below this thin band of fresher river water, clear (98–100) sea water still remained.

Oxygen

Oxygen data were too incomplete for a seasonal picture, but offshore waters were usually more highly saturated than inshore waters in the summer. Sound and marsh waters were usually unsaturated, see Ragotzkie (1960). However, offshore waters from station 2 out were always supersaturated (up to 135%) during the day sampling.

Convergences

Convergence (foam) lines are very common in Georgia, especially within the sounds and coastal water during ebb tide. During flood tide they tend to be destroyed but some are evident into high tide. In the sounds these lines seem to form where a tidal creek empties slightly different density water into the sound. Turbidity, salinity, and temperature were usually different on each side of the line which was almost always angular. How far under one of these masses may slide is unknown, but they probably go quite far at times and cause upwellings, temperature, turbidity, and salinity anomalies. For example, station 1 at the junction of three tidal creeks often had mid-waters at a different temperature than that of the surface and bottom.

Offshore these lines were perpendicular to the coast only at the mouths of inlets and the Altamaha River.

Water Masses

While this offshore convergence line is a convenient place to divide water masses, sometimes there were from 0 to 4 lines inshore of it parallel to the beach and sometimes no lines existed. The clear offshore area beyond 10 miles had low turbidity (95+), high salinity (over 30‰) and over-saturated oxygen in summer. Marsh water is usually brown and seldom extended beyond 4 miles although near inlets may go out to 8. One or two intermediate masses usually existed but their criteria was more subjective. Generally intermediate masses can

best be distinguished by turbidity (80–92%). Based on averages, offshore water was usually present from station 10 offshore, marsh water landward of 4. In between was what is here classed as coastal water.

On 19 August, 1965, a very thin (about 1 meter) band of cold salty water (36.3‰, 25.6°C) was found on the bottom of station 5. This was overlain by warmer, fresher water (27.8–28.2°C and 34.5‰), typical of most shelf water in the summer. This bottom-water had density characteristics of the water along the upper slope and lower continental shelf at the edge of the Gulf Stream off Georgia (Anderson, Gehringer and Cohen, 1956a, b). Green (1944) showed that water temperatures at Daytona Beach, Florida (about 120 miles to the south) were below 26°C in July and August whereas at Charleston and Savannah were about 28°C. He suggested upwelling of cooler water. Taylor and Stewart (1959) presented further evidence that this was due to upwelling. The edge of the shelf is only about 47 miles off Daytona while it is over 70 miles off Sapelo. The occurrence of this water within 20 miles of the coast must be short termed and perhaps very rare, although the intrusion is about as far inshore as at Daytona. It was never found during the remainder of the survey through the first week in August of 1966. The possible occurrence of this water should be sought to the south and seaward where this water mass may be intruding, but not upwelling.

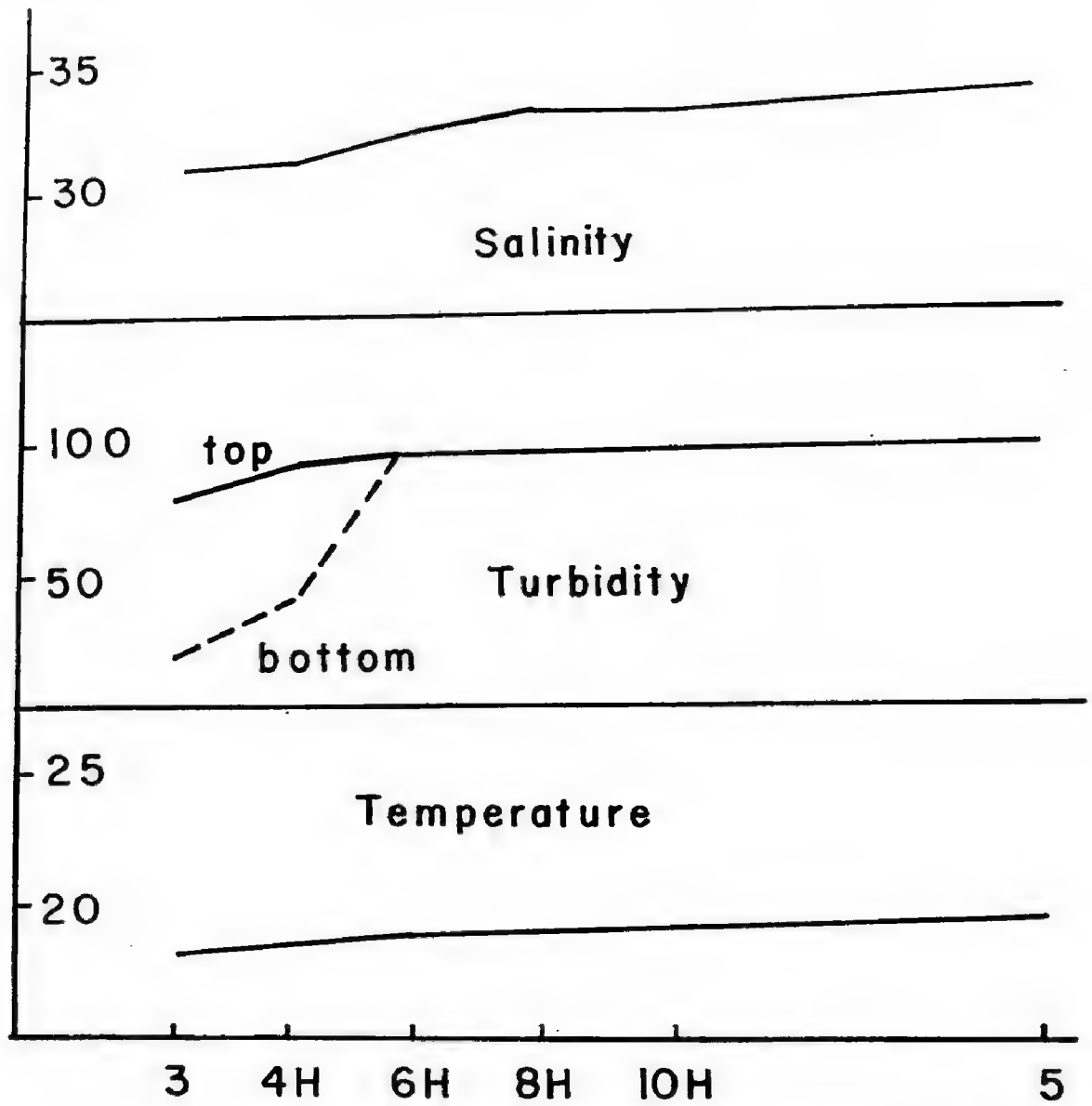

FIG. 4. Hydrographic cross-section through transect, 18 Nov. 1965.

Examples of three types of conditions encountered are shown. One type (Fig. 4) found on 18 November, 1965, shows nearly uniform conditions except for high bottom turbidity from station 6 inshore. Fig. 5, from the transect on 21 October, 1965, shows similar homogeneous conditions except high bottom turbidity extended to 8H; this is the farthest offshore muddy water was found. Several other transects were similar except for stratification. Fig. 6, on 22 March, 1966, shows a flood where surface salinities decrease seaward, due to the river pouring water out to sea to the south, spreading northward trapping ocean water landward.

These figures also show that the area of most rapid salinity and turbidity change revolves around station 6H.

CHARACTERISTICS OF THE FAUNA

The following discussion includes the more common species, usually those taken several times with a total of 20 or more individuals. Rarely caught forms are listed in Table 9 but a few noteworthy rare species are also discussed.

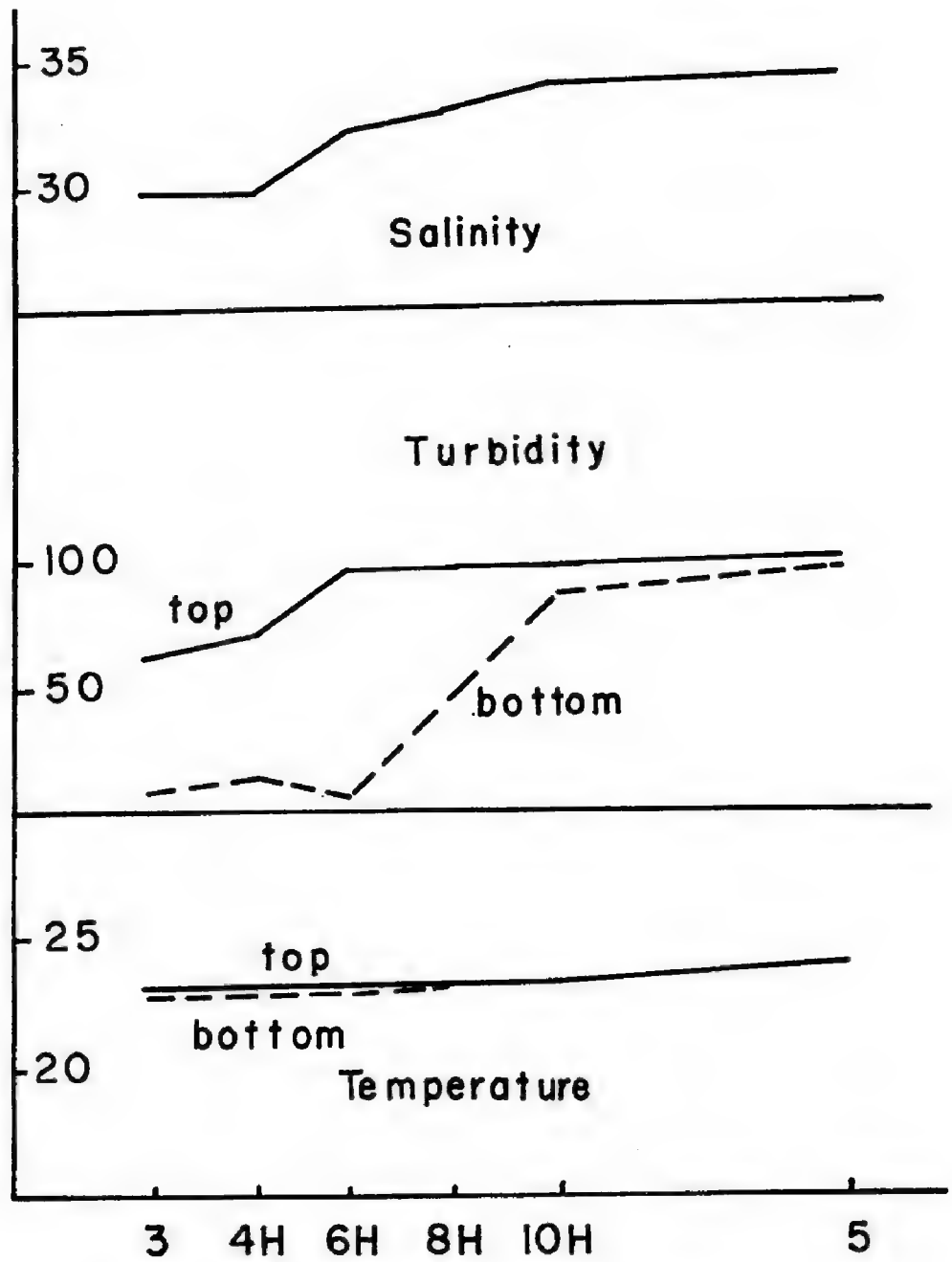

Fig. 5. Hydrographic cross-section through transect, 21 Oct. 1965.

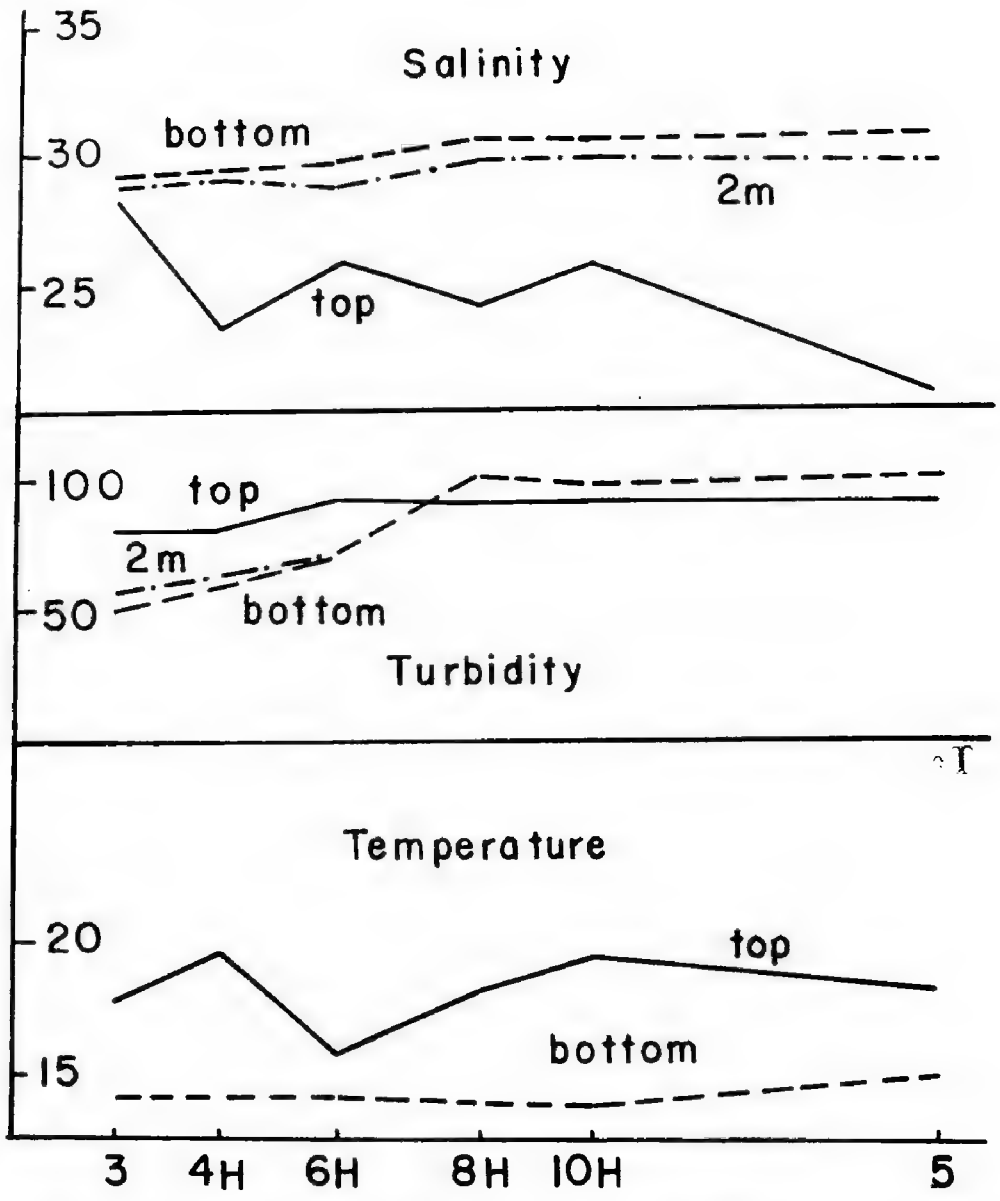

FIG. 6. Hydrographic cross-section through transect, 22 Mar. 1966.

Invertebrates

Tamoya haplonema—This jellyfish has been reported only sporadically but is known from Beaufort (Mayer, 1910). It is apparently not uncommon in Georgia, being found in all months except November and January through May. Seventeen (34–100 mm) were taken from stations 2, 3, 4H, 6H, 8H, and 10H.

Chrysaora quinquicirrha—Sea nettles were not especially widespread but 76 (4–16 cm) were found in September, October and July at stations 2, 4H, 6H, and 8H.

Cyanea capillata—The Lion's Mane occurred only from February through March, about the same time period it is known from the Gulf of Mexico (Hoese, Copeland and Miller, 1964). Ten (8–20 cm) were taken from stations 3, 4, 4H, 6H, and 8H.

Rhopilema verrilli—This large rhizostome was not previously known to be common south of Cape Hatteras, but is apparently a common member of the Georgia winter fauna. Large numbers were washed into Sapelo Beach from 27 January through 28 May. Thirty-five (11–60 cm) were taken from stations 2, 3, 4H, 6H, 8H, and 10H. Most were under 33 cm.

Beroe sp.—This ctenophore was evident through offshore waters except in

winter but was not always evident in trawls. It was never recorded landward of 6H.

Mnemiopsis sp.—This ctenophore is very difficult to identify in the water or in trawl samples. It was common from 6H to 10H in June and July but was undoubtedly more widespread.

Bugula sp.—An unidentified bryozoa was often abundant in sound trawl collections, especially in late winter and early spring.

Loliguncula brevis—Although this squid was found at all inshore stations, it was only abundant along the beach. especially at 3 and 4H. It seemed to prefer intermediate turbidities (70–90) and salinities (32–34‰) although found over a greater range. It appeared offshore only in February when *D. plei* was absent from the study area. The best interpretation of the data would be that *L. brevis* is limited seaward by competition with *Doryteuthis plei* and landward by high turbidities or salinities. Juveniles under 16 mm were taken only in June through November and under 10 mm only in June and July indicating a summer spawning season. Apparently this squid appears in the marsh very rarely only being taken once at station 7.

Size frequency data (Fig. 7) is very confusing. Spawning must occur primarily in the summer, but small individuals were taken almost year round. One egg case was found in July on the beach opposite station 2. The largest individual was 92 mm in mantle length.

Doryteuthis plei—This is not a well known squid, but was the common offshore species in the area, as it is in Texas. It was never taken farther inshore than stations 4H and 6H, and often not this far. It's landward penetration was closely associated with the penetration of clearwater (over 90%), but it may also be associated with absence of *L. brevis* (Fig. 8).

D. plei disappeared from the area in February when temperatures fell below 11°C. Although this is a tropical species, it was taken more commonly in the spring and fall. Whether this is due to decreased resistance to capture or actual abundance cannot be determined.

Length frequency data suggests late summer-early fall spawning and rapid growth through November, slowing through the winter (Fig. 9). There is no evidence that any live more than 1 year. The largest individual was 108 mm, but it is possible that some of the larger were confused with *L. peali*.

Squilla empusa—Mantis shrimp were most common offshore in 9–12 fathoms. However none were found there in the summer months (May–August). In the bay large numbers were taken at night in October, February and April. In August, however, few were taken during the day or night, and there was no marked nocturnal abundance.

The summer absence is not explained but may be related to spawning, because larvae and young were found only during the summer. This species constructs a crawfish-type burrow, where it apparently remains by day. Only two were taken in the upper Duplin.

Xiphopeneus kroyeri—Only 36 (69–109 mm) sea bobs were taken in September and October, and 2 in January. All were taken at station 3 off the beach. the same habitat the shrimp are commonly in in the Gulf of Mexico (Gunter, 1950).

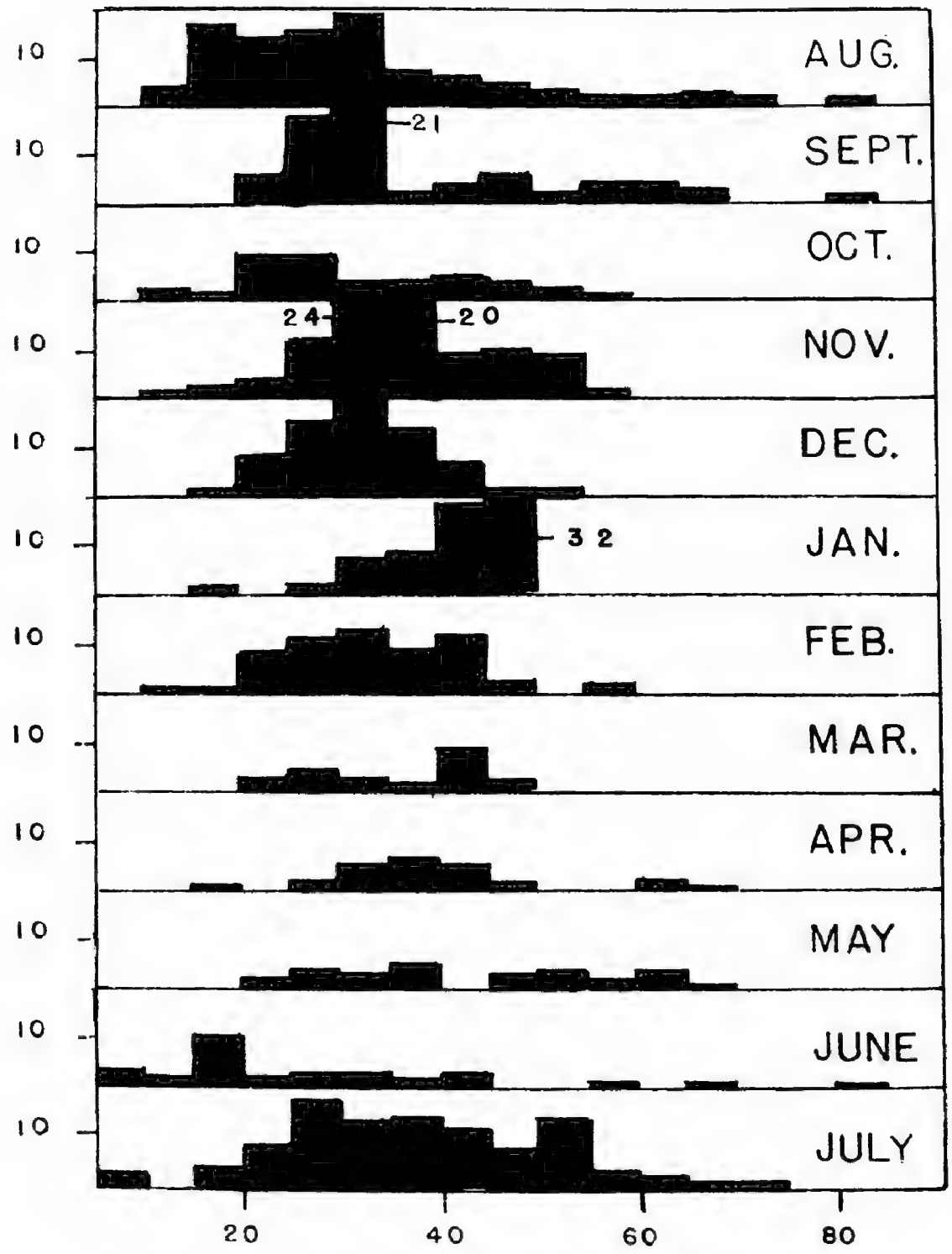

FIG. 7. Length frequencies by month for *Loliguncula brevis*.

Joyce (1965) found seabobs mostly from October through February off Florida. Anderson (1970) reported that seabobs were once much more common on the coast of Georgia.

Trachypeneus constrictus—This is a highly nocturnal species which was taken in large numbers at stations 3, 4, and 5 at night. During regular collections only 114 were found. The only juveniles under 30 mm were taken in June.

Off northeast Florida, Joyce (1965) found a similar pattern except he noted little evidence of nocturnal behavior. Anderson (1970) suggested a March–June spawning season in Georgia.

Penaeus duorarum—Pink shrimp are rare in Georgia and only 6 juveniles were taken in the present study, 2 from station 1, 1 from station 2, and 3 from Sapelo Sound. More may exist in saltier Sapelo Sound, but there is no evidence

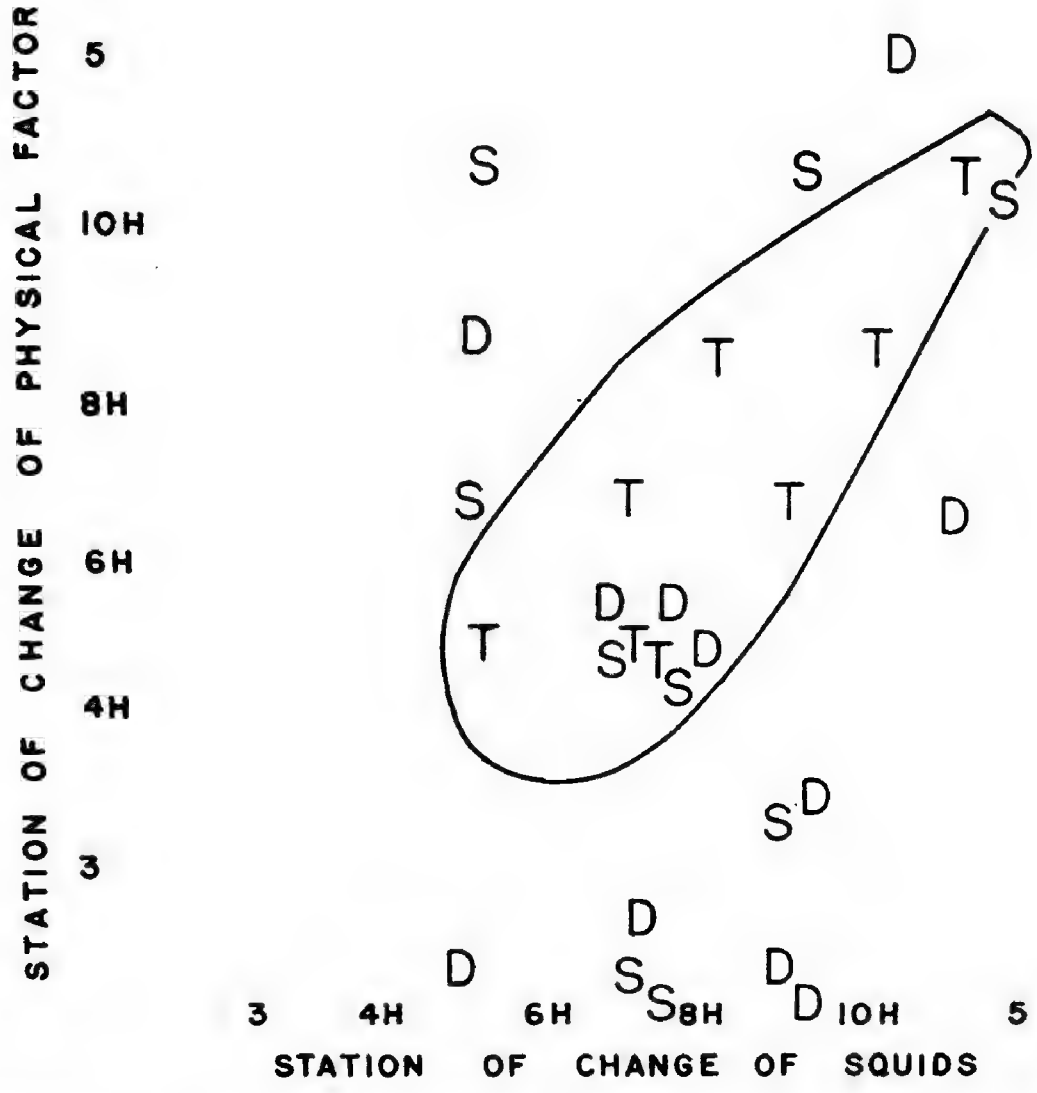

FIG. 8. Correlation of change of squid species with change of physical factor of the values: T = turbidity (90%), S = salinity (32‰), D = sigma-t (22). Solid line encompasses area where species and turbidity changes were always within. Arbitrary physical values were picked to represent most probable value to occur where squid species changed within the values occurring across transect.

of a larger population anywhere between North Carolina (Williams, 1955) and Northern Florida (Joyce 1965). Georgia landings show a small number of pink shrimp which are probably caught in Florida, as there is normally no recognition of the few that enter the local commercial catch. No adults are known from the area.

Penaeus aztecus—Brown shrimp were not very abundant but a definite pattern was evident. Juveniles, presumably from the marshes, entered the sound in June where 50 were taken at station 1. None were taken there in July, but a few (110–126 mm) appeared at station 2 in July 1965 and 3 in August 1965. In September a few appeared at 4H and at 6H in October (140–162 mm). This group then disappeared from the coast and no brown shrimp were taken again except for 19 (83–151 mm) from station 3 in January.

This second wave of sub-adults may represent a small fall peak of spawning. Fall spawning occurs both to the south (Joyce, 1965) in Florida and to the north (Williams, 1959) in North Carolina.

In summary, the following hypothesis for an annual brown shrimp cycle is as follows. A spring spawn appears with juveniles in the marshes moving to the

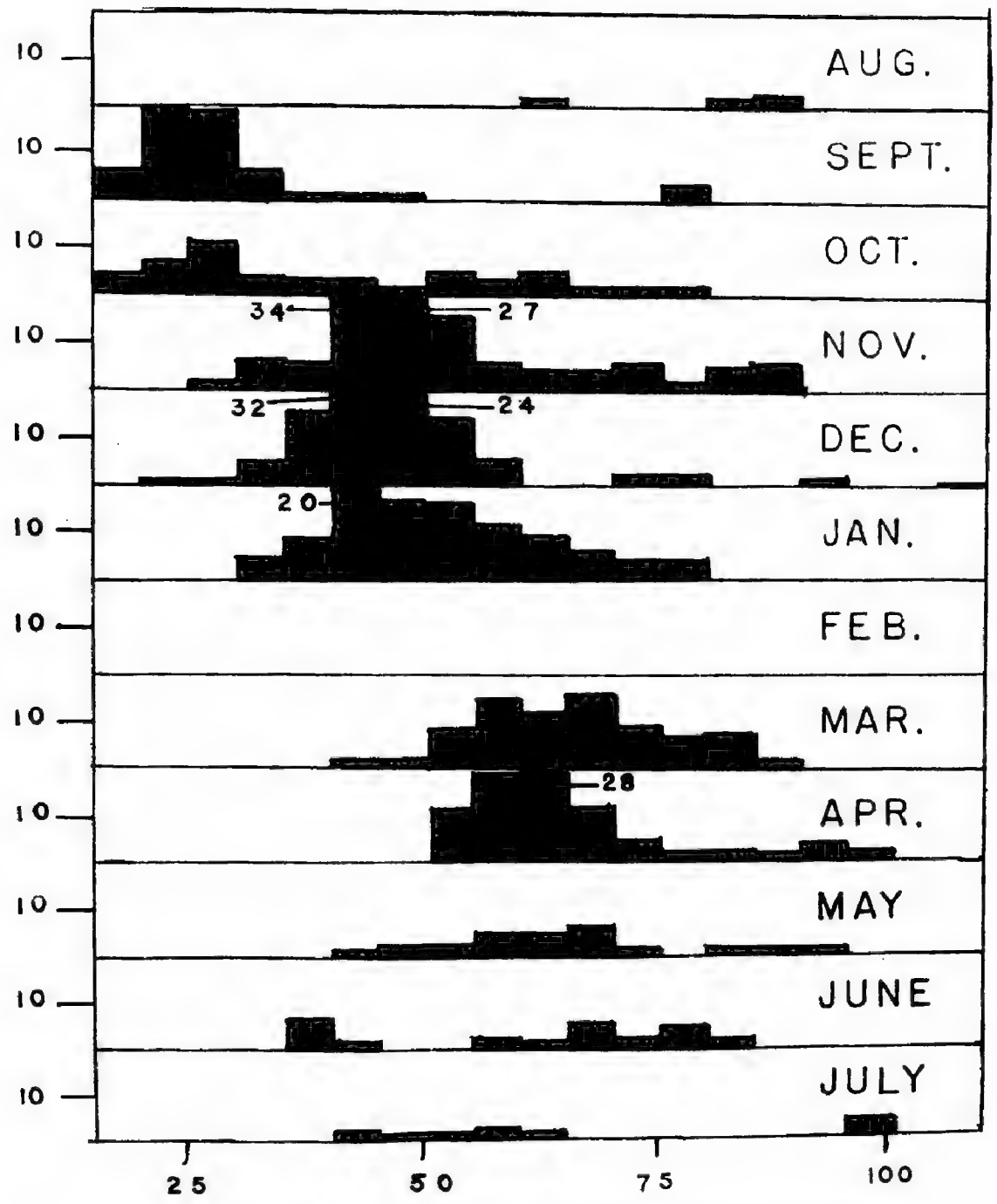

FIG. 9. Length frequencies by month for *Doryteuthis plei.*

sound in June and just offshore in July gradually working their way to about 6 miles offshore by October. There they disappear completely from the coast. Another very small wave of young comes from fall spawning, perhaps from shrimp spawning inshore, but it is obscured by the abundance of white shrimp. There is little evidence of overwintering and the spring influx of young probably come either from overwintering larvae from a fall spawn or from areas far from Sapelo Island.

Penaeus setiferus—White shrimp composed the major catch of Georgia shrimp and they are undoubtedly one of the most important members of the fauna. This is one of the few animals well studied in Georgia.

During the present study white shrimp appeared consistently at stations 1, 2, 3, 7 and 8, but never were found seaward of 6H, and seldom offshore of 3 or 4H.

Weymouth, Lindner and Anderson (1933) found ripe white shrimp in Georgia from April through September but they were scarce in the last four months. Early postlarvae were also found through this period.

TABLE 3

Invertebrate catch by dredge across transect during warm and cold month

Miles from beach	January 2	4	6	8	10	12	August 2	4	6	8	10
Callinectes sapidus	x	x	.	.	.	.	x	.	.	.	.
Callinectes similis	.	.	.	.	.	.	.	x	.	.	.
Portunus gibbesi	.	.	x	x	.	x	x	x	x	x	x
Ovalipes ocellatus	x	x	.	.	.	.	.	.	x	.	.
Ovalipes guadalupensis	.	.	x	x	x	x	.	.	.	x	.
Renilla sp.	.	.	.	.	.	.	x	.	.	.	.
Squilla empusa	.	x	x	.	.	.	.	.	.	.	.
Pagurus longicarpus	x	.	x	x	.	.	.	.	.	.	.
Pagurus pollicaris	x	.	x	x	x	x	x	x	.	.	.
Pagurus impressus	.	.	.	x	x	.	.	.	.	x	.
Trachypeneus constrictus	x	x	x	x	x	x	.	.	.	.	.
Polynices duplicata	x	x	x	x	.	x	x	.	x	.	.
Busycon canaliculatum	x	x	.	.	.	.	x	.	.	.	.
Oliva sayana	x	x	.	.	.	x	x	.	.	x	.
Sinum perspectivum	.	.	.	.	.	.	.	x	x	x	.
Spisula solidissima	.	.	.	x	x	.	.	.	.	.	.
Dinocardium robustum	.	.	x	x	.	.	.	.	.	.	.
Mellita quinquesperforata	.	x	.	x	x	.	x	x	x	x	.
Encope sp.	.	.	.	.	.	x	.	.	.	.	x
Cylpeaster subdepressus	.	.	.	.	.	x	.	.	.	.	x
Asterias forbesi	.	.	.	.	.	.	.	x	.	.	.
Luidia clathrata (Gray)	x	x	x	.	.	.	x	x	x	.	.
Luidia clathrata (Gold)	.	.	.	x	x	x	.	.	x	x	x

Length averaged 90 mm in July and reached 120–130 mm in the fall which is the peak of the commercial fishery. Size of the population decreased slightly through the winter but increased the next spring to form a second peak of large overwintering shrimp in April and May.

This was the most common animal taken in trawls, reaching its greatest abundance in the fall.

Portunus gibbesi—This was not an uncommon crab between stations 2 and 8H in the late summer and fall and appeared in most catches. Most ranged from 26–38 mm, but an ovigerous female (47 mm) was taken from station 5 in July. The fall young were probably from this spawn.

Ovalipes spp.—Two species of this crab were noteworthy in that *O. ocellatus* occurred usually at stations 3 and 4H and *O. guadalupensis* at 6H and offshore (Table 4). Although taken in most months they were not common in trawls, but dredge samples showed a similar distribution (Table 3).

Callinectes similis—This crab was common only in the fall, mostly at stations 2 and 3. Width ranged from 5 to 95 mm, but very small juveniles were found only in June.

Callinectes sapidus—Blue crabs are found predominantly in the marshes but

TABLE 4

Distribution by station in the transect of the commoner species

August, 1965–July, 1966

	3	4H	6H	8H	10H	5
Tamoya haplonema	x	x	x	x	x	.
Cyanea capillata	x	x	x	x	.	.
Rhopilema verilli	x	x	x	x	.	.
Trachypeneus constrictus	x	x	x	x	x	x
Penaeus aztecus	x	x	x	.	.	.
Penaeus setiferus	x	x	x	.	.	.
Squilla empusa	x	x	x	.	.	.
Callinectes sapidus	x	x	.	.	.	.
Callinectes similis	x	x	x	.	.	.
Portunus gibbesi	x	x	x	x	x	x
Ovalipes guadalupensis	.	.	x	x	x	x
Ovalipes ocellatus	x	x	.	.	.	.
Pagurus pollicaris	x	x	x	x	x	.
Mellita quinquesperforata	x	x	x	x	.	.
Cylpeaster subdepressus	.	.	.	.	x	x
Holothuria priniceps	.	.	.	.	x	x
Asterias forbesi	x	x	x	x	x	x
Luidia clathrata (Gold)	x	x	x	.	.	.
Luidia clathrata (Gray)	.	.	x	x	x	x
Loliguncula brevis	x	x	x	x	x	x
Doryteuthis plei	.	.	x	x	x	x
Raja eglanteria	x	x	.	x	x	x
Dasyastis sayi	.	x	.	x	x	x
Anchoa lyolepis	x	x	x	.	x	x
Anchoa hepsetus	x	x	x	.	x	x
Anchoa mitchelli	x	x	x	x	.	x
Synodus foetens	.	.	x	x	x	x
Diplectrum formosum	.	.	x	x	x	x
Lagodon rhomboides	x	.	x	x	x	.
Cynoscion nothus	x	x	x	x	x	.
Cynoscion regalis	x	x	x	x	x	.
Bairdiella chrysura	x	x	.	.	.	.
Stellifer lanceolatus	x	x	x	.	.	.
Larimus fasciatus	x	x	x	x	x	.
Leiostomus xanthurus	x	x	x	x	x	.
Micropogon undulatus	x	x	x	x	x	.
Menticirrhus americanus	x	x	x	x	.	.
Urophycis reguis	x	x	x	x	x	x
Hemipteronotus novacula	.	.	.	.	x	x
Rissola marginata	x	.	.	.	.	.
Trichiurus lepturus	x	x	.	.	.	.
Poronotus triacanthus	x	x	x	x	x	.
Symphurus plagiusa	x	x	x	x	.	.
Stephanolepis hispidus	.	.	.	.	x	x

		Number of species					
Invertebrates							
Not landward of		.	.	1	.	2	.
Not seaward of		.	1	4	3	2	.
Throughout	4	.	.	.	.	.	.
Fishes		.	.	.	.	.	.
Not landward of		.	1	2	0	2	.
Not seaward of		1	2	1	2	7	.
Throughout	5	.	.	.	.	.	.
Total	9	1	4	8	5	13	.

TABLE 5

Catch by month of common invertebrate species

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Total
Penaeus setiferus	1338	6634	1169	279	264	398	19	33	33	84	..	11	10262
Doryteuthis plei	4	5	49	91	651	49	..	75	440	24	23	11	1422
Loligunculo brevis		183	719	338	164	67	73	36	9	27	19	276	1955
Callinectes similis	36	346	881	17	5	1	..	..	2	..	5	9	1302
Callinectes sapidus	76	346	20	18	14	11	11	76	34	14	3	3	626
Portunus gibbesi	10	97	94	147	..	1	..	..	1	..	..	87	437
Luidia clathrata	17	1	..	4	4	8	..	1	..	..	1	..	36
Asterias forbesi	62	24	1	44	1	5	2	2	4	4	12	..	161

large catches were made offshore occasionally. No males were taken at station 3 and mature females were rare at stations 1 and 7. Width ranged from 41–191 mm, the largest an exceptionally large female. Sponge crabs were taken in July and August.

Asterias forbesi—Sea stars were taken only once at station 5, and occurrence at the other stations was sporadic with large numbers taken only once. There was little evidence of size groups, most measured between 29 and 110 mm, although the largest was 172 mm. However all specimens under 40 mm were taken between November and January.

Luidia clathrata—This starfish was sporadically taken year round with trawls, but was often common in dredge samples at all stations except in the sounds and station 2. Two color phases were present in the study area, a golden one offshore and a gray one inshore. The dividing line was very close to the 6 mile line as evidenced by collections at 6.4–6.1 miles offshore containing only the gold phase, and 6.0–5.6 only the gray phase, these distances determined by radar (see also Tables 3 and 4). The gray phase was taken four times as often as the gold.

INSHORE FISHES

Dasyatis sabina—This is not a rare stingray back in the marsh judging from several seen swimming there. However only 4 were taken in trawls, all in winter at stations 3, 4, and 4H. Gunter (1945) found this ray to move offshore in winter.

Lepisosteus osseus—Gars are much more common in the marsh than the two trawl captures in December at station 1 and March at station 7 suggest. In the Duplin gars were often seen breaking the surface.

Anchoa hepsetus—This anchovy seems adapted to coastal water with occasional forays into the saltier parts of the sounds, moving much as *Loliguncula brevis* did. 1504 were taken at stations 3 and 4. Size ranged from 33–113 mm.

Anchoa lyolepis—This uncommonly caught anchovy appeared sporadically throughout the year. Throughout the transect and at stations 3 and 4, 135 specimens ranged from 30–43 mm.

Anchoa mitchelli—Only 1293 were taken at two stations in Doboy Sound in contrast to 5941 at station 3. Occurrence farther offshore than station 4H was limited to the cold months (October–March). Modes shifted from between 33

mm in August, 44 mm in September, 52 mm in October, to 56 mm in November where their size remained nearly constant with a slight drop in mode back to nearly 50 mm through the winter until July when another group (mode 29 mm) appeared (Fig. 10). These data suggest a summer breeding season with rapid growth to adult size by fall, movement slightly offshore in winter, with maturity reached the following spring with rapid disappearance after spawning. The largest individual captured was 78 mm. *A. mitchelli* appeared sporadically in the Duplin but was common from October through December in shallow water at station 8, which is the only time anchovies appeared in abundance at station 1.

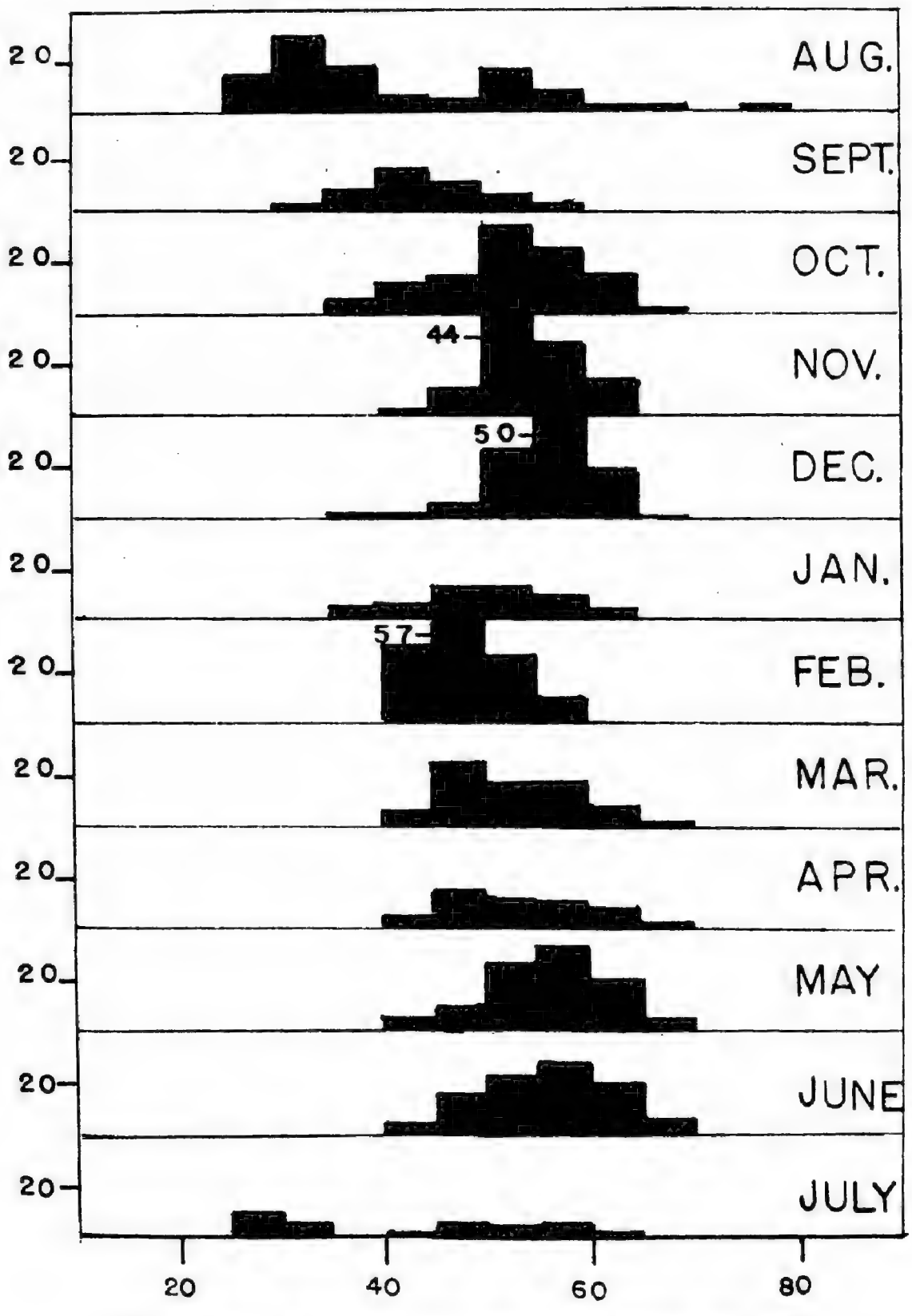

FIG. 10. Length frequencies by month for *Anchoa mitchelli*.

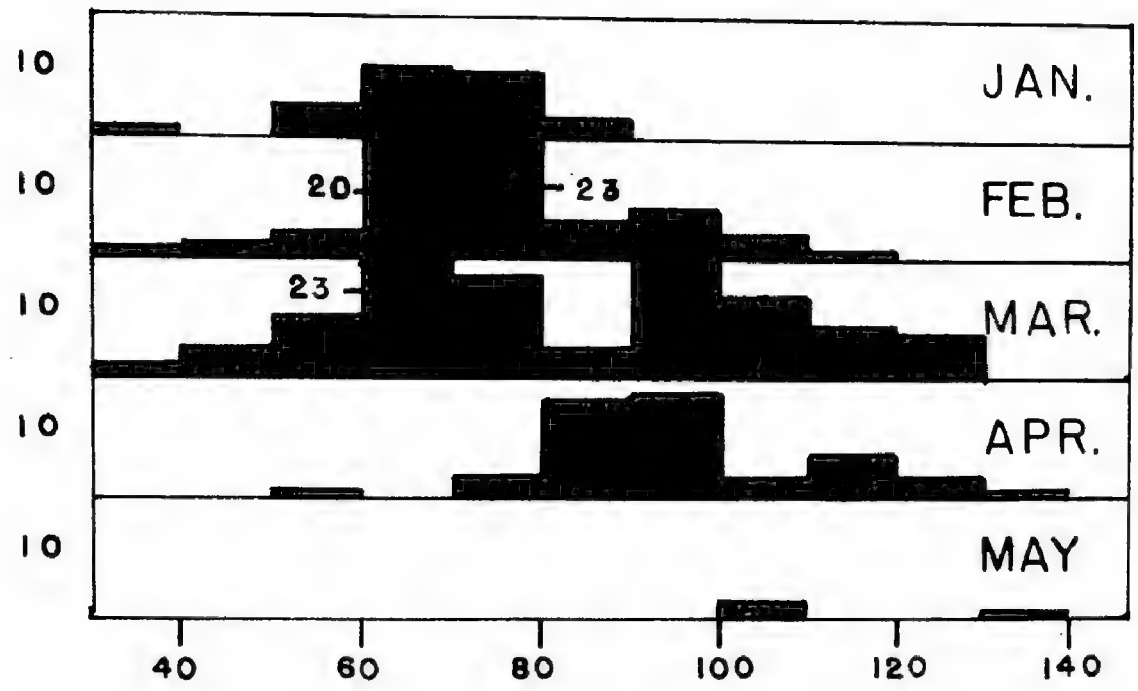

FIG. 11. Length frequencies by month for *Urophycis* spp.

Urophycis sp.—The species identified in later catches was *regius* but it is possible that another species was mixed in the catches as was found off Texas (Miller, 1965) and reported in Georgia by Dahlberg and Odum (1970). Young appeared inshore in February and size increased steadily to 109–149 mm in May when they evidently all disappeared seaward (Fig. 11). However, while common early in winter, most probably left by the end of April and recruitment seemed to be continual through March. They occurred at all stations between 1 and 5.

Trachurus lathami—Rough scad apparently occurred sporadically in a narrow band from 6H to 10H, including station 4. One hundred and thirty-two were taken there in October and March–April. Size ranged from 51–124 mm.

Chlorosombrus chrysurus—Apparently large schools of bumper were occasionally encountered from August through September with 298 taken from inshore of 8H and 2 at 5. Young under 25 mm were taken in August and September. Maximum size was 135 mm.

Centropristis philadelphica—This sea bass was taken only rarely, but year round. The smallest specimen (29 mm) was taken in June, but the rest were 91–120 mm from stations 1, 2, and 3.

Bairdiella chrysura—Silver perch were more common back in the marsh but large individuals (81–136 mm) were taken in the sound and inshore area, occurring beyond station 3 only in December and March.

Larimus fasciatus—Banded croaker were largely limited to stations 3 through 4H, but appeared as far out as 10H in October. Young under 35 mm were taken in August through October at 3 and 4H.

Leiostomus xanthurus—Spot were very common in the shallow water of the marshes and only six small ones (23–29 mm) were taken in the sound in April. In the Duplin, young spot (38–91 mm) were abundant in the summer and completely absent from October through February.

In May large numbers (50–76 mm) appeared in the sound and these were apparently represented by larger (71–119 mm) ones at station 3 in June, while

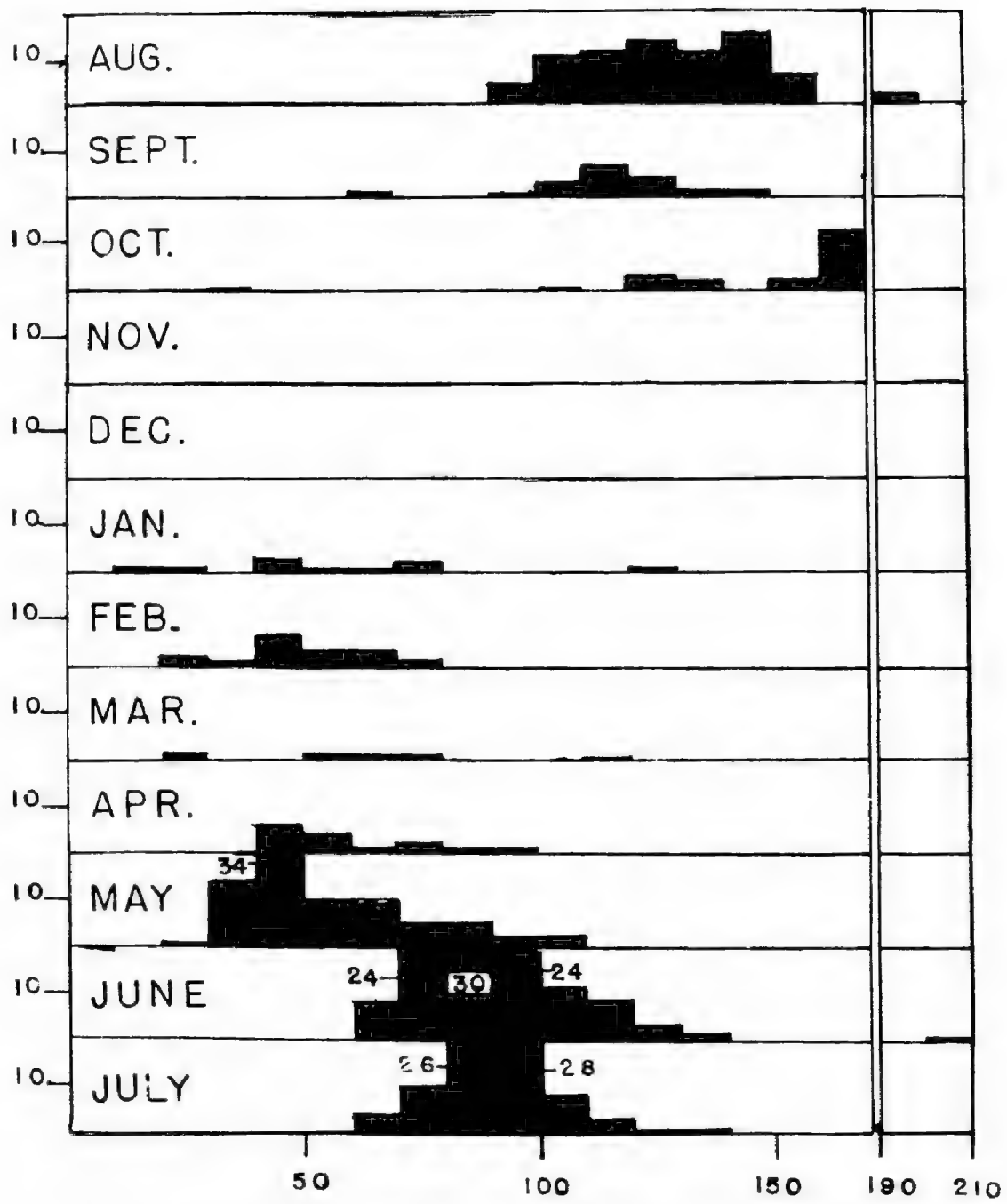

FIG. 12. Length frequencies by month for *Micropogon undulatus*.

another group (54–75 mm) appeared at station 1 in July. These merged with larger ones which apparently became widespread in the fall. Large ripe males (158–172 mm) were taken at 10H, 8H and 4 in October and December.

Micropogon undulatus—Young croaker under 30 mm were taken in Doboy sound in December through February and May. These apparently grew rapidly (Fig. 12) reaching 8–9 cm in July. Georgia croaker apparently reach 12–13 cm in less than one year and disappear from the inshore trawl catches.

A group of 14 (167–170 mm) ripe male and female croaker were taken at 10H in October and 3 other large ones (16–20 cm) were taken offshore of 4H in the early fall preparatory to spawning. What happens to these croaker is a mystery, unless they are very scarce. It is not impossible, as Hansen (1970) seems to have found, that croaker reach maturity in one year, and older croaker are insignificant if present at all. Very large croaker might represent individuals from very early spawns. Some croaker do reach 150 mm in about 12 months, so possibly some reach 50 mm more in 14 months. However, the occasional summer capture

of large croaker suggests that a few survive to the second year, but grow only 50 mm in 8 months or so.

Since trawls probably select for slower moving fishes any growth curve should flatten as the fish grow both from the effects of slowed growth and the selectivity of the trawl. This is suggested by data indicating greater ability of larger croaker to avoid trawls (Hoese, Copeland, Moseley and Lane, 1968).

Stellifer lanceolatus—The star drum is perhaps the characteristic fish of the sounds. Spawning apparently occurs in summer as specimens under 20 mm were taken only in June through September. These had a modal size of 36 mm in July, 46 mm in August, 51 mm in September, and 56 mm in October where it remained until February, but shrinking slightly in March. In April a group of large star drum (79–106 mm), previously poorly represented, appeared commonly until the fall. During the winter they were seldom caught but reappeared in March.

Although common at 4H and inshore they were taken only once at 6H (October), never at 7, and only 71 from the shallow water of station 8.

A suggested life cycle of star drum in Georgia is summer spawning with rapid growth until winter, slow growth through the winter until spring. There is a suggestion in length frequency data (Fig. 13) that two size groups sometimes existed, but whether this represents two spawnings in the same or different years cannot be judged from the data. In either case few seem to survive over 1 year. These data agree essentially with those presented by Dahlberg and Odum (1970) for two nearby sounds.

These data also agree essentially with those of Gunter (1945), who interpreted the large fish present in spring as those surviving 2 winters.

Menticirrhus americanus—Although this was a frequently occurring fish, an inadequate number was taken to determine growth rates. Most ranged from 56 to 203 mm. One of the largest was a ripe male taken at station 2 in August and a juvenile (24 mm) was taken in September at 7. Whiting were taken only twice (October) offshore of 4H.

Cynoscion regalis—Sea trout were one of the commoner fishes. Specimens under 50 mm were taken in June through September in the inshore area and in the Duplin. The species was scarce in winter and early spring but young (19–76 mm) were common in summer. Size ranged from 26–246 mm.

Cynoscion nothus—This trout was much rarer and appeared only once at station 1 (in October). Size ranged from 43–196 mm. *C. nothus* were taken at 8H and 10H in October but otherwise the species was restricted to inshore of 6H.

Trichiurus lepturus—Cutlass fish were common inshore but never appeared seaward of station 4H. Specimens over 400 mm (up to 639 mm) appeared only in May through August and young (141–274 mm) were taken only at station 3 in November and again after a winter absence in April with none smaller than 226 mm seen in the summer.

Rissola marginata—This was not a common species although night collections would probably reveal its abundance. Seven (53–128 mm) were taken between November and February at stations 3 and 4H.

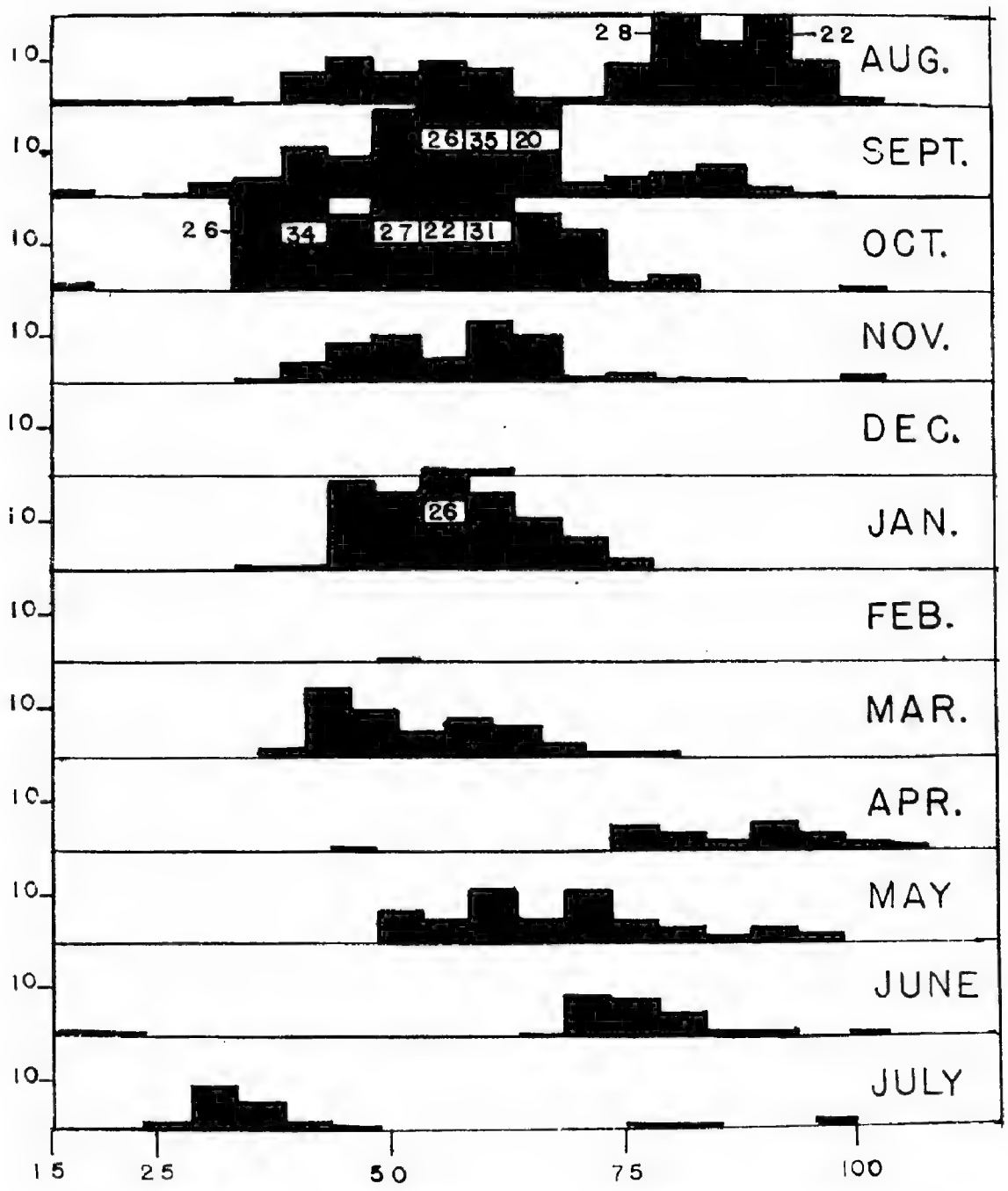

FIG. 13. Length frequencies by month for *Stellifer lanceolatus*.

Peprilus alepidotus—Harvestfish were not common but were taken inshore in most months. Seventy-six ranged from 31–102 mm.

Prionotus tribulus—Sea robins were taken as far offshore as 6H, but they were never common with only 36 taken at regular stations. Most were young, with the smallest (17–21 mm) taken in September–October.

Etropus crossotus—Although rarely found as far off as station 10H this small flatfish was most common at station 2. Size ranged from 60–129 mm, except for one (23 mm) taken in May from station 8. A summer absence is unexplained, but might be related to spawning.

Symphurus plagiusa—Tonguefish were limited to the inshore area, appearing offshore of 4H only in October. They constantly appeared inshore but the numbers varied widely. Most ranged from 41–153 mm with smaller sizes (under 80 mm) taken only in December through March, but 1 (18 mm) was taken from station 1 in August.

OFFSHORE FISHES

Carcharhinus acronotus—A single individual (455 mm) was taken at station 10H in May. Except for *Squalus* this was the only shark taken at regular stations.

Squalus acanthias—This was the only abundant large animal in the winter, 17 taken in January and February. All were females (66–86 mm) taken at stations 4H, 6H, 10H, 3 and 4.

Raja eglanteria—All clearnose skates were taken between October and April; 15 (16–28 cm) at stations 3, 4H, 6H, 8H, and 10H.

Dasyatis sayi—Fourteen adults and one juvenile were taken between November and April, all at stations 8H, 10H, 4, and 7.

Myliobatis freminvilli—This ray was encountered only twice. Three (47–69 cm) taken from 10H in November and 1 (67 cm) from 4 in April. Bearden (1965) reported several from nearby South Carolina.

There seems to be a winter concentration of elasmobranchs between 2 and 10 or so miles from the coast, which includes 2 rays and 1 shark, all of which are common summer species north of Cape Hatteras. It is interesting that Anderson (1968) reported neither *Myliobatis* nor *Squalus* from extensive catches made during the early 1930's.

Synodus foetens is somewhat puzzling because it was not found at the stations inshore of 6H, and only there in the summer, but was taken in saltier Sapelo Sound. It was found only in salinities above 31.8‰. Lizard fish were most common in the late fall and spring. Size ranged from 63 to 304 mm, but most were between 10 and 20 cm.

Diplectrum formosum was usually present at the offshore stations, although it was uncommon in winter, only two taken during January through March, contrasted with 36 the remainder of the year. Size ranged between 64 and 178 mm. Taken only three times inshore of 10H, it was present in over 50% of offshore catches.

Lagodon rhomboides is a common species over much of the southern United States coast, but is very rare in inshore Georgia. Inshore of station 6H only two (78–101 mm) were taken early in the study, although a few other juveniles were seen in seine hauls. Also, it was not reported in the extensive collections of Dahlberg and Odum (1970).

However, in April, 412 juveniles (27–54 mm) were taken at station 4, 247 at 10H, 4254 at 8H, and 1138 at 6H, but none inshore of this. In May only 6 (53–68 mm) were taken at station 4, and 13 at 10H and 8H. By June none were found. Relatively few came inshore although one (78 mm) was taken at station 3 in July and a few were seen in seine hauls in June near the beach. For some reason, pinfish avoided the inshore waters. Several authors (see Caldwell, 1957) have shown the association of pinfish with submerged vegetation and the absence of inshore submerged plants may help explain the dearth of pinfish.

Hemipteronotus novacula is a secretive species known for its ability to bury (Breder, 1951). It was taken from April through November, but was common only in August. Size ranged from 22 to 146 mm but the smaller sizes (under 75 mm) were found only in September and November. It appeared at 10H only in September.

TABLE 6

Catch by month of most common fish species

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Total
Diplectrum formosum	41	9	3	9	6	3	..	..	9	9	1	6	96
Hemipteronotus novacula	23	14	1	1	..	..	..	..	6	..	5	4	54
Synodus foetens	.	..	14	10	13	1	3	..	8	4	..	1	54
Stephanolepis hispidus	5	..	10	..	..	..	..	..	..	4	3	9	31
Anchoa mitchelli	3330	1216	444	791	74	53	159	191	429	386	67	131	7271
Urophycis sp.	.	..	.	.	.	33	72	126	63	3	..	..	297
Etropus crossotus	4	..	28	1	35	13	1	52	1	3	..	..	138
Symphurus plagiusa	30	507	323	67	62	86	3	137	23	13	17	6	1274
Cynoscion nothus	50	.	64	20	12	..	1	..	5	24	6	8	190
Cynoscion regalis	474	207	101	66	23	63	2	3	1	13	25	71	1049
Bairdiella chrysura	7	150	104	32	4		..	..	6	14	..	..	317
Stellifer lanceolatus	1086	5428	935	2142	2	207	1	103	27	177	75	26	10209
Menticirrhus americanus	119	6	17	27	31	59	2	6	2	27	13	17	326
Micropogon undulatus	314	439	57	..	8	69	19	11	45	256	366	127	1711
Leiostomus xanthurus	77	..	1	..	7	..	..	..	6	331	57	96	575
Trichiurus lepturus	12	46	..	37	3	..	..	2	173	130	20	7	430

Stephanolepis hispidus was another warm water species, found between May and October. Except for 3 (70–88 mm) taken in August and one (46 mm) in October all were large (138–197 mm). This species spawns in the vicinity of the Gulf Stream and young apparently make their way inshore, first hiding amongst leaves of sargassum. Inshore of the Gulf Stream vicinity sargassum was usually absent and there was little surface debris for protection. In this band inshore to about 10H in August and September young hid in the bell chamber of the ctenophore *Beroe*.

INSHORE—OFFSHORE FAUNAL CHANGES

The changes apparent in the fauna progressing from the muddy sounds into the ocean are very striking (Table 4). Two immediate possibilities may explain these changes—(1) the differences in properties of the water masses, (temperature, salinity, turbidity, etc.) or (2) changes in the character of the bottom. Two other apparent changes occur—depth and distance offshore. It so happens that the area of most rapid change in the bottom is also the area where the demarcation of the water masses fluctuate, possibly because they influence each other or some of the properties of the water mass are caused by the same factors that influence the bottom sediments. This line is about at 6H, with addition of large amounts of shell and coarse sand seaward and fine sand landward. Actually coarse sand does not become entirely predominant until just beyond 10H, an area not intensively investigated. Pilkey and Frankenberg (1964) place the relict-recent boundary (where the sand changes to coarse) at just under ten miles at my transect but grab samples suggest it is closer (Table 1). Some fine sand occurs farther out on the shelf, but it is not so evident.

Of common animals collected (Table 4) many occurred neither seaward nor landward of 6H. However, the change is a gradual one and not limited to a strict area. However, many of the species occurred only once beyond 6H and then at a particular season. For example, all the sciaenids were usually landward of 6H, but several species were taken 4 miles farther seaward during spawning season in October when the inshore mass was the farthest seaward ever. Of the species not listed in Table 4, 37 occurred only at 6H and landward, 29 at 8H and seaward, and only 7 across 6H and 8H.

Of the species occurring throughout the transect most were pelagic. One benthic form, *Luidia clathrata*, changed color phases at about the six mile line. Of the other bottom forms, only *Portunus gibbesi*, *Asterias forbesi*, and *Raja eglanteria* were found throughout the transect. Over the whole year more pelagic forms were found over a greater range, but on any one day were more restricted. The best example of this were the squids, *Loliguncula brevis* and *Doryteuthis plei* (Fig. 8). Although *D. plei* never penetrated farther landward than 6H, *L. brevis* moved over the whole area in February and *D. plei* disappeared, apparently due to low temperature. These two squids overlapped only in July when both were taken at 8H and 10H. Usually (4 samples) they were not taken together or (5 samples) overlapped only at one station. This is easily explained by the trawl moving from the offshore squid into schools of *L. brevis*.

Distribution in the transect of these squids correlates fairly well with turbidity, especially in that *D. plei* was never found in waters muddier than 90%. The squid boundary line during the year moved from between 4H and 6H to 10H and once moved completely out of the study area. With the exception of February this boundary followed the turbidity boundaries closely. This would suggest two possibilities. Either *D. plei* is limited by turbidities less than 90% and forces *L. brevis* landward because of competition or some factor associated with the different water masses (which are correlated best with turbidity) serve to separate the two species. Some combination is also possible since it is likely that both species have some way of recognizing differences between the water masses.

The inshore fauna on the Georgia coast is clearly a warm temperate one, but immediately offshore becomes at least somewhat subtropical, especially during the warmer months. The predominance of penaeid shrimps, certain portunid crabs, and sciaenid fishes is comparable to areas to the north (Hildebrand and Schroeder, 1928), as well as the northern Gulf of Mexico (Gunter, 1945, 1950; Reid 1954). Therefore the inshore-offshore faunal break tends to separate temperate and tropical faunas. Some exceptions do occur in that some tropical forms are found in the sounds at times and some temperate forms move far offshore, the former more in the warmer months and the latter more in the colder months. Some cold temperate forms, such as *Squalus* and *Cancer* move into the area only during colder months, (see Table 9).

The fauna seems to bear more relationship to that of Louisiana than of any other area. White shrimp, *Penaeus setiferus*, and star drum, *Stellifer lanceolatus*, are also characteristic of Louisiana inshore waters (Gunter, 1938). Both areas have large amounts of marsh, highly turbid waters, and large expanses of mud bottoms. There are many exceptional differences, however, and the habitats of

the two areas differ significantly, despite a basic quantitative similarity in the faunal list.

Comparison of this study with two others on fishes in the area (Dahlberg and Odum. 1970; Anderson, 1968) showed few important differences. Anderson (1968) collecting in 1933–35 caught much fewer *Symphurus plagiusa* compared to the later studies but caught relatively more *Etropus crossotus*, which ranked number 4 in his inside list but only number 12 in mine and number 11 in Dahlberg and Odum's. Anderson caught large numbers of *Chlorosombrus chrysurus* in outside waters, perhaps indicating a greater abundance at that time. Also, *Galeichthys felis* was taken commonly by both Anderson (No. 6 in Sounds) and Dahlberg (No. 4) but was only an incidental species in my study. Other differences can be easily explained by collecting gear and/or location.

ABSENCE OF GRASS BED FLORA AND FAUNA

The Georgia-South Carolina salt marsh system is unusual in its lack of submerged spermatophytes and macroscopic algae. No evidence of submerged grass beds were found from Fernandina Beach, Florida to Georgetown, South Carolina. The northernmost range of the sea grasses in Florida has not been determined. but several species are common south of Cape Canaveral (Phillips, 1960; Moore, 1963; den Hartog. 1970). A small amount of *Ruppia maritima* occurs in Georgia at the boundary of fresh waters and in fresh water, but none has been found in the estuaries. Healthy. living turtle grass, *Thalassia testudinum*. plants with entire roots with leaves were found floating at the surface at station 5 in October, but none came inshore. One species of grass, *Halodule beaudetti* (*Wrighti*) occurs both north and south of this salt marsh system (Moore, 1963), ranging no farther south than *Zostera* at Beaufort, North Carolina (den Hartog, 1970).

Neither are communities of macroscopic algae common. Small amounts of *Ulva* were sometimes found in shallow waters close to the inlets and along the outer beaches. A few plants of red and brown algae were found sporadically from 10 to 60 miles offshore. but these were always small and not well developed. Although macroscopic algae probably occurs sporadically in many places there are no large communities of plants.

Also absent with the plants are the large assemblages of animals associated with them (Moore. 1963). Many of the species common in grass beds are either absent or rare on the Georgia coast. The bay scallop. *Aquipecten irradians*, has never been found in Georgia to my knowledge. Pink shrimp and pinfish. (common resident species of southern grass beds) are rare in Georgia, which contrasts sharply to their dominance in areas where grass beds abound. Other species expected in trawl catches are rare in Georgia presumably due to the absence of grass beds. One species. *Lucania parva*, a common fish in grass beds of the Gulf and middle Atlantic states, while not expected in trawl catches, also seems to be absent from Georgia. It may occur in fresh water, but it does not seem to be a member of the salt marsh or sound margin community.

Although the absence or rarity of these species seems associated with the absence of grass beds. the parameter of the community provided for each of these

species is known only in a few cases. Also some common grass bed species are, nevertheless, common in Georgia. For example, speckled trout, *Cynoscion nebulosus*, common in grass beds (Guest and Gunter, 1958) of the Gulf and Atlantic states is a common Georgia fish. Apparently removal of grass beds does not provide the necessary limiting factor for some species.

From a zoogeographic point of view the presence of such a long stretch of unbroken salt marsh may provide enough of a barrier to disrupt distributions or perhaps gene flow of certain species. Matanzas Inlet, Florida is given as a separation point in species of fishes of the genera *Chasmodes* (Springer, 1959) and *Fundulus* (Miller, 1955). There has been little work in this area and the northern limit of some grass or algal communities' probably occurs somewhere along this coastline.

The limiting factor for the plants seems to be turbidity. There is no evidence that the salt marsh system has prevented north-south dispersal of any organism that is capable of withstanding the temperature extremes of either side, but it seems to prevent development of abundant resident populations of many species within the area. It may interrupt some gene flow and certainly prevents many forms from extending as far north or south as their temperature tolerance would allow.

TOTAL CATCH

The catch by weight after preservation was converted to grams per m^2 of the area the trawl was estimated to travel over. This distance was computed from a mean distance traveled calculated by radar which results in some error, since the actual distance trawled apparently varied about ±20% from the mean. Nevertheless, this error is much smaller than others involved, such as what percentage of animals in the area trawled are actually caught and how representative of a large area a single sample is. Some confidence is placed in reproducibility because the two offshore stations (4 and 5) and the two inshore stations (2 and 3), while differing in any one month, over a whole year were remarkably similar in both the invertebrate and vertebrate catch (Table 8).

The catch in the sound was about 8 times that offshore and about twice that inshore. The standing crop inshore-offshore ratio of fishes, however, was somewhat lower and that of the invertebrates higher. This is due to the prevalence of tunicates, bryozoa, shrimp, and crabs in the sound, which brought the invertebrate catch to weigh as much as the fishes. This is in contrast with all other stations where the fish biomass was 2–5 times as great as the invertebrates.

The offshore decrease occurred very rapidly, usually seaward of station 3, sometimes at 4H. Stations 8H and 10H usually had catches similar to 4 and 5. The inshore abundance falls within marsh water, and apparently diminishes rapidly in coastal water. This supports the view of a productive salt marsh with less productive water seaward. However, the break seems to be a sharp one, as is also the transition between water types. There is certainly little evidence from the biomass of trawl caught animals that much marsh water escapes seaward.

According to the experience of Hoese et al, (1968) day trawling in clear water can be very misleading. Two night cruises offshore in October and February

TABLE 7

Day-night catches at selected stations

	NIGHT Station 5 October Invert.	Fish	February Invert.	Fish
Number of species	5–5	9–9	7–7	0–5
Number of individuals	58–32	42–58	32–53	0–181
	Station 4 Invert.	Fish		
Number of species	24	1		
Number of individuals	158	1		
	DAY Station 5 October Invert.	Fish	February Invert.	Fish
Number of species	3	7	1	4
Number of individuals	4	41	7	11
	Station 4 Invert.	Fish		
Number of species	2	4		
Number of individuals	6	16		

yielded a few more species but no great increase in numbers (Table 7) except in some clearly nocturnal species such as *Trachypeneus*. The offshore catch would probably be greater at night, but further study is needed to determine how much. Even if the offshore biomass is actually as high as the day-night differences given by Hoese et al (1968, Fig. 5), it is still much below that of the inshore waters. The differences between the day-night invertebrate catches seemed larger (Table 7) agreeing with the data of Hoese, Copeland, Moseley and Lane (1968). Even with these corrections the offshore standing crop seems to be far below that inshore.

The offshore catch (about 3 pounds per acre) is somewhat below that computed by Hildebrand (1954, 1955) for shrimp grounds in the western Gulf of Mexico. The inshore Georgia catch (Table 8) is similar to the yearly average of 2.3 gms/

TABLE 8

Total catches converted to area

	Invertebrates Avg. weight in gms/m^2	Avg. No./m^2	Fishes Avg. weight in gms/m^2	Avg. No./m^2	Total Avg. weight in gms/m^2	Avg. No./m^2
Sta. 5	0.05	0.063	0.26	0.022	0.31	0.085
4	0.11	0.102	0.20	0.123	0.31	0.225
3	0.26	0.21	0.92	1.51	1.18	1.72
2	0.31	0.19	0.98	0.86	1.29	1.05
1	1.26	0.42	1.32	1.62	2.58	2.04
Avg.1,2,3	0.61	0.119	1.07	0.419	1.68	0.538
Avg.4,5	0.08	0.083	0.23	0.073	0.31	0.155
Total Avg.	0.40	0.104	0.74	0.280	1.14	0.385

m^2 found by Hoese and Jones (1963) in Texas grass beds, but is far below the average of about 130 lbs/acre reported for the Texas Laguna Madre (Hellier, 1962). However, he caught many fast-moving fishes that are not often caught in trawls.

Total numbers of trawl caught animals may be in some way related to the total biomass present in an area. A total of 14,069 animals were taken in 12 hours of trawling, about 1172 animals per hour and 0.4 animals per m^2. Concentrations varied from one animal every 12 m^2 at station 5 to one animal every 1.3 m^2 at station 3. Trawl efficiency is probably low.

POTENTIAL COMMERCIAL FISHERIES

While most of the present fisheries seem restricted to close inshore, there may be areas offshore Georgia where certain species congregate. These are hard substrate areas, characteristically containing large numbers of sponges, gorgonians, and tunicates. Most of these areas are far offshore and difficult to reach. They have not been adequately explored, but are worthy of study both for academic reasons and for potential fisheries. Station 4 often contained hard substrate species, but apparently had only an irregular bottom.

The possibility of a trash fish fisheries receives little support from this study. First, there is only a relatively narrow zone available and it overlaps completely with the shrimp fishery. Catches in the sounds might be adequate, but this would take large numbers of juvenile shrimp. Areas close to the beach (stations 2 and 3) only twice had catches of fish in excess of 500 lbs/hr and averaged only about 180. This is close to figures presented by Roithmayer (1965) for the industrial bottomfish grounds east of the Mississippi Delta but somewhat below his average.

Midwater trawling and night fishing might discover concentrations of fishes offshore, but presently the only known significant abundance lies inshore of a line usually 3 or 4 and seldom beyond 6 miles beyond the beach. Night fishing might increase the catch somewhat, perhaps not significantly, but this is an area needing further study.

CONCLUSIONS

There is a great deal of evidence of an inshore-offshore break on the middle Georgia coast occurring between 6 and 10 miles off the barriers. This view is supported by the standing crop of fishes and invertebrates, the distribution of many species of both, differences in sediment type, and differences in water masses. The causes of the faunal changes are related to the latter factors, which may be in turn related to each other. Pelagic species distribution seems to be correlated with water masses, but other factors may also be involved. Benthic forms seem primarily tied to bottom type, but again their distribution may be controlled by other factors also.

Undoubtedly the high productivity of the salt marsh is the primary factor allowing a much larger biomass to develop inshore. Apparently this richer water is kept close inshore and relatively little nutrient leakage occurs. Most nutrients in the marsh seem to be tied up in detritus, which is closely restricted to the

TABLE 9

Rarer species

Species	No.	Months	Stations	Size (mm)
Aurelia aurita		September	4H	65
Pelagia cyanella	6	July	2.3	3–7cm
Chiropsalmus quadramanus	2	July	2,4	
Renilla sp.	4	August	3	19–29
Polynices duplicatus		Oct., Nov.	4H	
Sinum perspectivum	5	Jan.–Mar.	3.4H–6H	
Rossia sp.	1	April	4	16
Loligo peali	2	April–May	4.5	132–157
Octopus vulgaris	1	May	4	93
Limulus polyphemus	4	Feb.–May	4H,2	25–58cm
Alpheus heterochaelis	2	Feb., June	1	32–46
Periclimes sp.	Many	July	2	
Pagurus impressus	1	October	5	
Pagurus pollicaris	11	Year-round	4H–10H.2.3,4	
Clibinarius vitattus	1	March	1	
Parthenope sp.	1	January	8H	
Podochela sp.	1	April	10H	
Aranaeus cribarius	3	Aug., Oct.	4H	76–116
Portunus spinimanus	5	Dec.–April	2.4	34–58
Hepatus epheliticus	7	May–Sept.	2–3,4	23–83
Cancer irrorata	3	April	4	22–31
Astropecten duplicatus	3	Feb.–April	8H.10H.5	
Libinia emarginata	2	Jan.–April	8H.6H	
Astropecten articulatus	5	Year-round	10H.5	
Arbacia punctulata	11	Sept., Feb., April	10H.4	
Lytechinus sp.	1	November	4	60
Ophiopholis elegans	5	Aug., Nov.	6H,4	
Clypeaster subdepressus	7	Sept., Jan.	5	92–111
Encope sp.	3	May–June	4	26–28
Thyone sp.	2	March	2.1	
Holothruria priniceps	9	May, Aug., Nov.	10H.5	60–82
Molgula sp.	15	Feb.–May	8H.10H.4.5	
Carcharhinus acronotus	1	May	10H	46cm
Sphryna lewini	1	May	2	88cm
Opisthonema oglinum	1	June	3	114
Trachinocephalus myops	1	October	5	104
Ophichthus gomesi	3	June, Sept., Oct.	1.2	447–500
Ictalurus catus	3	March	1	117–202
Fistularia tabacaria	1	November	5	211
Centropristes striatus	4		2.6H,8H	77–83
Hemicaranx amblyrhynchus	1	July	5	113
Trachinotus carolinus	1	October	3	164
Vomer setapinnis	18	Sept., Nov.	1,3	
Scomberomorus maculatus	1	October	4	178
Lutianus campechianus	1	August	4	46
Cynoscion nebulosus	2	Jan.–Feb.	1,4	136–252
Stenotomus sp.	3	Mar., Sept.–Jan.	10H	81–101
Upeneus parvus	2	May, April	10H,8H	
Orthopristis chrysopterus	1	October	8H	134
Eucinostomus gula	11	Aug., Oct., Nov.	8H–10H	60–96

Species	No.	Months	Stations	Size (mm)
Gobiosoma ginsburgi	1	September	4	17
Hypsoblennius hentzi	1	March	2	71
Otophidium welshi	1	October	6H	
Otophidium omostigium	1	October	8H	
Poronotus burti	26	Sept.–May	3,4H–10H	27–96
Sphryaena guachanche	6	Aug., Sept.	3	59–121
Opsanus tau	1	January	1	118
Bothus ocellatus	1	August	4H	84
Citharichthus spilopterus	1	September	2	79
Paralichthys lethostigma	7	Mar., Aug., Oct., Dec.	1,2	(127–335)
Paralichthys dentatus	2	May, June	2	(68–223)
Scophthalamus aquosus	3	Dec., May, Aug.	10H,4,2	(63–79)
Syacium papillosum	2	Aug., Oct.	5	177–193
Ancylopsetta quadrocellata	23	Mar.–May, Aug., Nov.	1,2,3,4,5,10H	51–209
Pomatomus saltatrix	5	Apr., May, July, Nov.	1,2,3	67–176
Trinectes maculatus	8	Oct., Mar., May, Aug.	1,2,3	54–130
Gobiesox strumosus	1	December	1	46
Alutera schoepfi	3	May	4	(351–371)
Acanthostracion quadricornis	1	May	10H	
Prionotus scitulus	24	Year-round	1,10H,4	46–98
Prionotus carolinus	11	Mar., Oct., Nov.	6H,10H,4,5	58–131
Chilomycterus schoepfi	1	June, Nov.	2,4	31–141
Ogcocephalus sp.	7	November	5	38–56

inshore area. Although fresh water may be diffused into the offshore area it apparently carries little detritus as evidenced by turbidity and the distribution of loose, decaying *Spartina*, which was rare in the offshore area.

There may be times, however, when inshore water is carried offshore and rapidly diluted. During strong offshore winds clear water has been observed near the beach perhaps due to upwelling after coastal water is blown offshore. Some sampling was done during offshore winds, however, without finding any evidence that this extends beyond 8 or 10 miles. Further study between 2 and 12 miles off this coast should yield important information about the interaction of species, both between themselves and their environment.

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OBSERVATIONS ON THE HYDROLOGY AND MARINE ORGANISMS OF THE TIDAL COLORADO RIVER AND ADJACENT WATERS, TEXAS, FEBRUARY–JUNE 1962

Richard A. Diener[1]

National Marine Fisheries Service Biological Laboratory, Galveston, Texas 77550

ABSTRACT

Salinity and temperature measurements and collections of organisms at 2-week intervals began in February, 1962 and continued through June, 1962 at 10 stations in the tidal Colorado River of Texas and adjacent waters.

Surface salinity ranged from 1.0‰ (parts per thousand) to 31.2‰ and bottom salinity ranged from 10.6‰ to 31.2‰. Surface salinity fluctuated the most in the Colorado River, increasing with flood tide and decreasing with ebb tide while the least fluctuation occurred in East Matagorda Bay, reflecting the reduced influence of tides and high evaporation-precipitation ratio. Surface and bottom salinity differences were the greatest (28.5‰) in the river and the Gulf Intracoastal Waterway where mixing was slight, and the least (8.4‰) in the bays where mixing was the greatest.

Water temperatures (surface and bottom) paralleled the general warming trend of air temperature. Temperatures of bottom waters during February and early March were warmer than those of surface waters, but the situation reversed itself during the remainder of the study.

Eighteen species of invertebrates and 39 species of vertebrates were collected. Ctenophores, brown shrimp (*Penaeus aztecus*), and blue crabs (*Callinectes sapidus*) were the most abundant invertebrates while the Atlantic croaker (*Micropogon undulatus*), spot (*Leiostomus xanthurus*), and sand seatrout (*Cynoscion arenarius*) were the most abundant vertebrates. Nearly all of the abundant species displayed numerous peaks within the study area during May or June with a corresponding increase of size as the season advanced from February to June.

INTRODUCTION

Published information on the hydrology and biology of the Colorado River-Matagorda Bay area is limited and fragmentary. Galtsoff (1931) described the salinity regime and oyster producing areas in Matagorda Bay. Shenton (1957) studied the foraminifera and bottom sediments of Matagorda Bay, and Marland (1958) studied the ecology of the molluscan fauna. Day (1959a, 1959b, 1961a, and 1961b) listed 44 forms of invertebrates and 98 vertebrates that were collected in Matagorda Bay.

[1] Contribution No. 325, National Marine Fisheries Service Biological Laboratory, Galveston, Texas 77550.

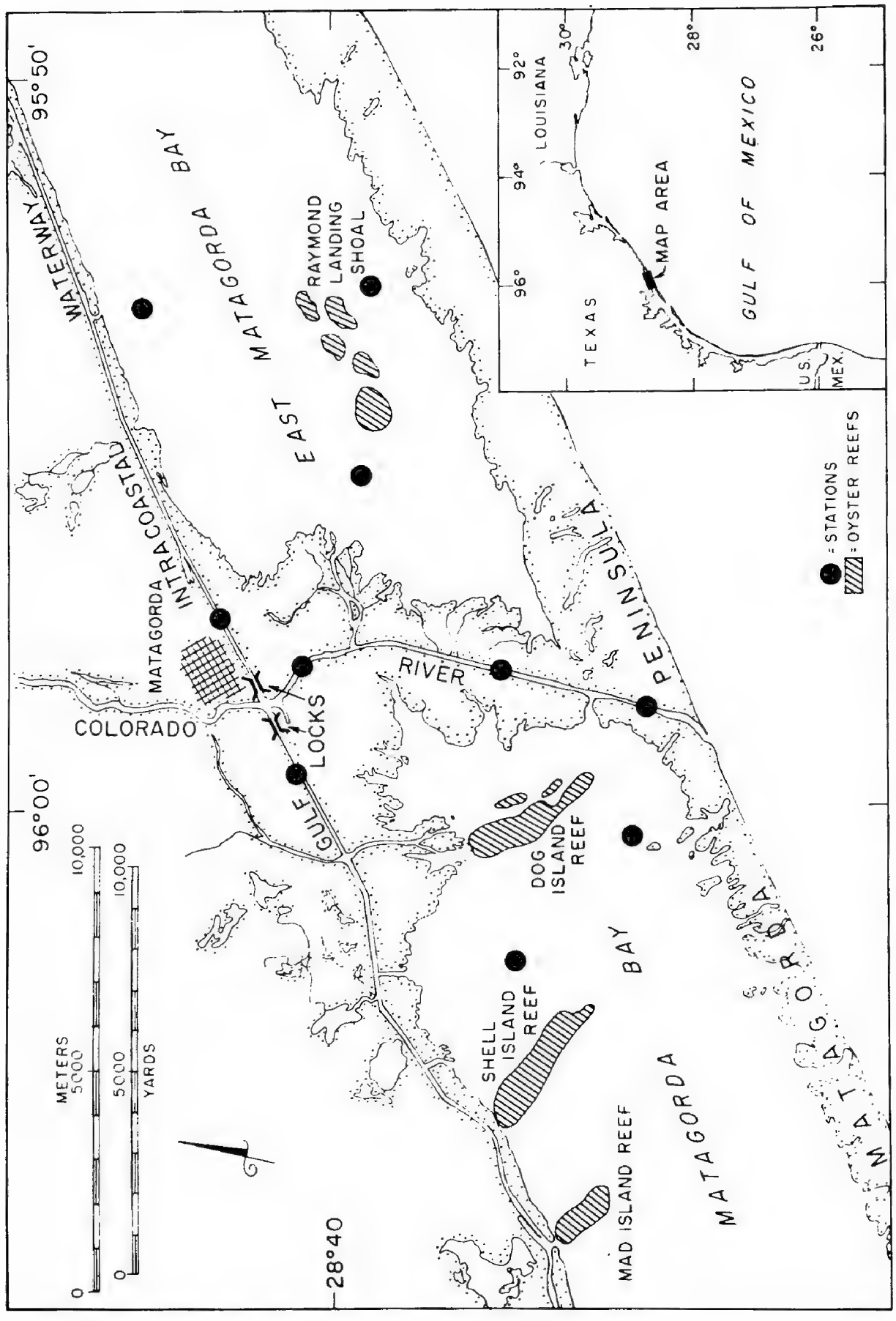

FIG. 1. The Colorado River Delta, Texas and adjacent waters with locations of 10 hydrographic and biological sampling stations.

In general, the literature on Matagorda Bay does not treat the eastern arm, tidal reaches of the Colorado River, Gulf Intracoastal Waterway, or East Matagorda Bay as extensively as it does the bay proper.

This description of the hydrology and the faunal components of these waters in late winter and spring is offered as a contribution toward a more comprehensive understanding of the environmental and biological characteristics of the Matagorda Bay area.

The Study Area

The Colorado River Delta, formed after 1924, bisects the original eastern arm of Matagorda Bay into two distinct bays (Fig. 1). These two bays are further subdivided superficially by several oyster reefs. Two of these reefs—Shell Island Reef in the eastern arm of Matagorda Bay, and Raymond Landing Shoal in East Matagorda Bay—approximate the western and eastern limits of the study area. The widths of the two bays are as great as 8 km and the distance between the two reefs is about 18 km.

Depths at mean low water are similar in the two bay areas. East Matagorda Bay has a relatively flat featureless bottom with depths at many points as great as 1.5 m at mean low water (m.l.w.); depths averaged about 1.1 m. East of Shell Island Reef, Matagorda Bay has a relatively level bottom with a maximum depth of about 2.1 m and an average of about 0.9 m.

The Gulf Intracoastal Waterway and the river channel have uniform depths of 3.7 m (m.l.w.) that are maintained by dredging. Surface width of the Waterway is about 45 m; width of the river ranges from 90 m along most of its length through the delta to about 115 m at the point of junction with the Waterway. Maintained bottom widths of the river and the Waterway are about 38 m.

The range of diurnal tides in the Matagorda Bay area varied from about 0.2 m to nearly 0.4 m in 1962 (U.S. Coast and Geodetic Survey Tide Tables, 1962). Continuous winds for several days, however, affect the predicted time and heights of the tides. Reid (1955) noticed this phenomenon during his investigations in the estuaries northeast of Galveston, Texas.

MATERIALS AND METHODS

Measurements of salinity and temperature and collection of organisms at 10 stations began at 2-week intervals in February, 1962 and continued through June, 1962. The stations were in four bodies of water that represented three basic habitat types: the tidal reaches of a river, a man-made waterway, and adjacent segments of two bays. Three stations were in the Colorado River, two in the Gulf Intracoastal Waterway, two in the eastern portion of Matagorda Bay (hereafter referred to as Matagorda Bay), and three in East Matagorda Bay. Total observations in each area are listed in Table 1.

Salinity and temperature were measured in surface and bottom waters. Surface temperatures

TABLE 1

Number of hydrographic observations and trawl hauls by habitat, February to June 1962

	Colorado River	Gulf Intracoastal Waterway	Matagorda Bay	East Matagorda Bay
	Number	Number	Number	Number
Salinity:				
Surface	32	20	18	26
Bottom	32	20	18	26
Temperature:				
Surface	32	20	17	24
Bottom	31	20	15	23
Trawls:	32	20	18	25

were obtained by reading a centigrade thermometer held in a bucket of freshly drawn water. Bottom temperatures were obtained similarly after the water was collected with a 400-cc Kemmerer water sampler. Salinities were determined in the laboratory by a modification of the Mohr-Knudson titration method described by Marvin, Zein-Eldin, May, and Lansford (1960). Tidal readings were taken at the staff gauge on the Colorado River locks at Matagorda.

Marine organisms were collected with a try-net. The net, with an opening of 3.0 m, was towed behind an outboard skiff for 10 minutes over a distance of about 450 m. The stretched mesh size of the wings of the net was about 3.5 cm and that of the bag or cod-end about 2.5 cm. Trawl doors measured approximately 29.2 by 66.0 by 2.5 cm.

Measurements of fish and invertebrates, other than shrimp and crabs, were of total length in millimeters. For fish, this measurement represents a straight line from the tip of the snout to the end of the tail with the caudal rays squeezed together. Carapace widths of crabs were measured and analyzed separately by sex. Penaeid shrimp were weighed to the nearest gram.

HYDROLOGY

Salinity

The data suggest that the salinity regime of the study area is complex, characterized by wide ranges and frequent fluctuations. Salinities of surface water samples ranged from 1.0‰ to 31.2‰ and those of bottom waters from 10.6‰ to 31.2‰ (Table 2). Fluctuations in salinities differed markedly between the four habitats studied (Fig. 2).

Much of the flow of the Colorado River enters directly into the Gulf of Mexico, however, small amounts enter the Gulf Intracoastal Waterway and eastern Matagorda Bay. Of these bodies of water, tidal influence is strongest in the Colorado River where fluctuations in surface salinities were the greatest, increasing with flood tide and decreasing with ebb tide. Salinities were lowest near the Gulf Intracoastal Waterway and highest near the mouth. Fluctuations in bottom salinities were not as great, and values were generally higher than in surface waters. Indications of seasonal increase or decrease in salinity values were not apparent in either surface or bottom waters.

During the study, the mean monthly discharge of the Colorado River at Bay City ranged from 341 to 1,183 cfs (cubic feet per second) (9.65 to 33.49 cu. m per second) and averaged 768 cfs (21.74 cu. m per second) (U.S. Geological Survey, 1962). This flow was considerably lower than the 14-year average of 2,541 cfs (71.95 cu. m per second), and fluctuations in discharge could not be correlated with salinity.

In the Gulf Intracoastal Waterway, salinities of surface and bottom waters fluctuated markedly with no apparent seasonal trend. Fluctuations were similar at the surface and bottom. Average bottom salinities ranged from 14.6‰ to 25.1‰ and were generally lower than any of those recorded in the other three habitats.

In the two bay areas, salinities generally increased during the study. Exceptions to this seasonal trend occurred in Matagorda Bay in early May and June when an intrusion of fresh water lowered average salinities. In East Matagorda Bay, however, fluctuations in salinities were less than in any other area. This body of water was not directly influenced by any appreciable source of fresh or salt water. Salinities gradually increased with little variation, a feature unlike the other three habitats. Such a trend may be ascribed, in part, to reduced influ-

TABLE 2

Ranges of salinity and temperatures by month and habitat in the Colorado River Delta area, February–June 1962

Water body	February ‰	February °C	March ‰	March °C	April ‰	April °C	May ‰	May °C	June ‰	June °C
Colorado River										
Surface	2.5–30.6	13–19	2.3–10.3	13–19	3.7–25.0	18–23	1.3–29.6	26–28	1.0–13.3	30–31
Bottom	15.8–31.0	14–20	17.5–26.3	14–17	20.8–28.3	18–22	21.0–29.9	25–28	12.8–28.2	28–30
Gulf Intracoastal Waterway										
Surface	14.7–15.2	19–20	9.2–21.2	14–21	15.7–24.7	19–23	8.9–22.8	24–28	7.8–12.3	29–30
Bottom	15.7–16.9	20	17.5–22.0	13–19	19.1–26.4	18–22	11.7–23.3	23–28	10.6–22.6	27–30
Matagorda Bay										
Surface	*	*	17.4–26.3	12–21	22.9–27.9	18–24	18.8–31.2	26–28	16.3–27.8	30
Bottom	*	*	18.5–26.8	12–20	26.3–28.0	18–24	20.4–31.2	26–28	17.3–27.9	29–30
East Matagorda Bay										
Surface	17.5	21	18.9–22.5	13–19	21.5–26.0	19–23	23.3–27.9	24–26	25.7–27.9	27–29
Bottom	17.9	22	21.1–22.6	14–16	22.5–26.0	19–23	23.5–28.1	24–26	26.2–28.1	27–29

* No data.

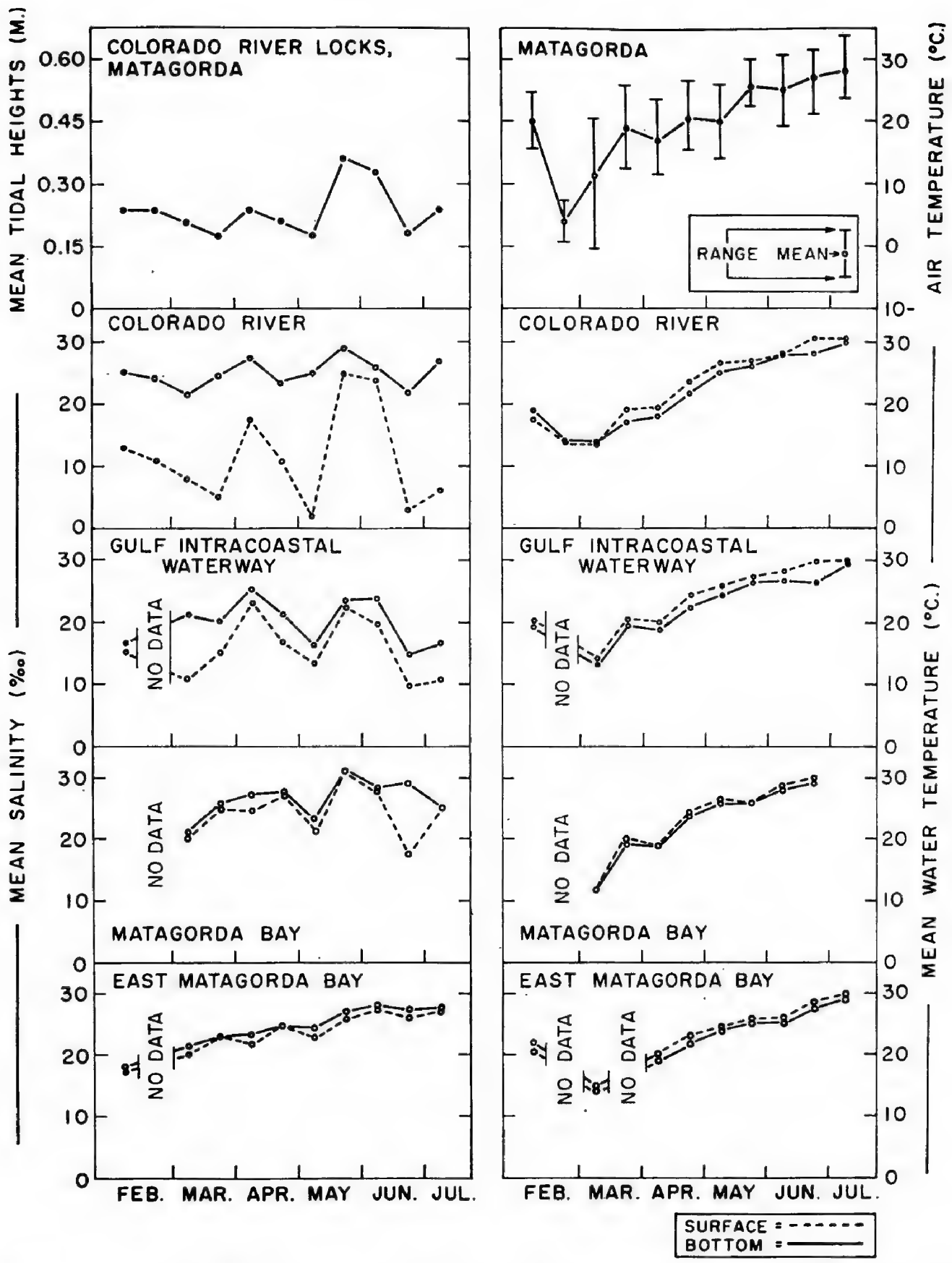

FIG. 2. Average salinity and temperature (surface and bottom), tidal heights, and air temperatures in the Colorado River delta area, on sampling dates, February-June 1962.

ences of tides, low rainfall (according to the U.S. Weather Bureau, about 55 mm, or 2.2 inches, below the normal of 371 mm or 14.1 inches for the February-June period) and increased evaporation (Collier and Hedgpeth, 1950).

Differences between surface and bottom salinities measured simultaneously were greater in the channel habitats than in the two bays. At certain stations in the Colorado River and Gulf Intracoastal Waterway, differences were as great as

28.5‰, whereas in the two bays they were no greater than 8.4‰. This condition may be attributed to the fact that the broad and shallow bays are more affected by wind-driven waves that mix surface and bottom waters than are the narrow and deeper river and Waterway channels.

Temperature

Unlike salinities, surface and bottom water temperatures followed similar patterns throughout the study area and were related to air temperature (Fig. 2). At no time did surface water temperature deviate more than 3°C from that of bottom water. The 3°C difference was noted in simultaneous surface and bottom readings at stations in the Colorado River and the Intracoastal Waterway. Surface temperatures in February and March were generally cooler than bottom temperatures, but these conditions were reversed when air temperatures increased and stabilized during the remainder of the study.

Air temperature (converted to °C from U.S. Weather Bureau data for Matagorda, Texas) on sampling dates dropped from an initial high of 24.5°C in February to a low of 0.5°C in early March (Fig. 2). Air temperature then gradually increased until a high of 33.5°C was recorded in June. This trend was paralleled by surface and bottom temperatures.

FAUNA

Eighteen species of invertebrates and 39 species of vertebrates were collected in a series of 95 try-net samples. One invertebrate, a ctenophore, was taken in such large numbers that enumeration was impossible. Of the remaining forms, six species of invertebrates and eight species of vertebrates were abundant enough to be considered as "common." These accounted for 13,748 individuals or 97.1% of the total catch of 14,155 individuals (Table 3).

Analysis of size data of the common forms indicated that few small or large individuals, notably fish under 15 mm or over 150 mm, were taken in the try-net. The paucity of small individuals reflects escapement through the large mesh net, whereas large individuals may have either escaped the net or moved to waters of generally higher salinity as they approached maturity. This latter phenomenon with respect to approach of maturity was described by Gunter (1945, 1950) for fish and invertebrates inhabiting coastal waters of Texas.

Invertebrates

The six common invertebrate forms listed in Table 3 represent about 98.5% of all invertebrates, exclusive of ctenophores. Of these, the brown shrimp (*Penaeus aztecus*), the blue crab (*Callinectes sapidus*), and the white shrimp (*P. setiferus*) constitute much of the volume and value of the Texas commercial fishery harvest. All of the common invertebrates listed have been reported in the diets of such fish as the spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogon undulatus*), and the sand seatrout (*Cynoscion arenarius*).

With the exception of the ctenophore, the invertebrate taken most frequently

TABLE 3

Grouping of 17 invertebrate and 39 vertebrate forms taken by trawling during February–June 1962

	Total catch
INVERTEBRATES (exclusive of ctenophores)	
Common forms:	
Penaeus aztecus	3,606
Callinectes sapidus	611
Palaemonetes spp.	319
Penaeus setiferus	299
Callinectes similis	277
Sergestidae, unid.	198
Uncommon forms:	
Lolliguncula brevis	47
Portunus sayi	9
Euphausiidae, unid.	6
Squilla empusa	5
Macrobranchium ohione	5
Penaeus duorarum	2
Trachypenaeus constrictus	1
Xiphopenaeus krøyeri	1
Neopanope texana	1
Ovalipes ocellatus	1
Maiidae, unid.	1
VERTEBRATES	
Common forms:	
Micropogon undulatus	5,545
Leiostomus xanthurus	1,602
Cynoscion arenarius	508
Lagodon rhomboides	233
Brevoortia patronus	169
Anchoa mitchilli	163
Arius felis	113
Citharichthys spilopterus	105
Uncommon forms:	
Symphurus plagiusa	51
Porichthys porosissimus	51
Paralichthys lethostigma	49
Stellifer lanceolatus	30
Polydactylus octonemus	21
Urophycis floridanus	19
Bairdiella chrysura	19
Sphoeroides parvus	18
Trinectes maculatus	9
Menticirrhus americanus	8
Achirus lineatus	7
Prionotus tribulus	6
Dasyatis sabina	5
Pogonias cromis	4
Archosargus probatocephalus	4
Chaetodipterus faber	4
Gobionellus hastatus	3

	Total catch
Gobiesox strumosus	3
Synodus foetens	2
Cynoscion nebulosus	2
Gobiosoma bosci	2
Mugil cephalus	2
Bagre marinus	1
Orthopristis chrysopterus	1
Trichiurus lepturus	1
Gobioides broussonneti	1
Microgobius spp.	1
Astroscopus y-graecum	1
Hypsoblennius ionthas	1
Ancylopsetta quadrocellata	1
Monacanthus hispidus	1
Total	14,155

was *Penaeus aztecus* (Tables 3 and 4). This is the most valuable single species taken by the commercial fishery of Texas. Overall, the brown shrimp ranked third in abundance behind ctenophores and *Micropogon undulatus*. *P. aztecus* was first collected in April and reached a numerical peak in late May which was followed by a decline in June. This species displayed a gradual weight increase between April and June; the weight of specimens taken in April ranged from 0.6 to 2.2 g and averaged 0.8 g, while the weight of those taken in June ranged from 0.6 to 9.7 g, averaging 1.8 g. Specimens as heavy as 18.4 g were taken in May, but the greatest abundance of individuals under 2.0 g held the average to 1.4 g.

The third ranking invertebrate was *Callinectes sapidus* which also enters the sport and commercial fishery of Texas. The blue crab was collected throughout the study area with the greatest catches made in early April (Table 4). The size (width) of 265 males increased, with those taken in February ranging from 11 to 61 mm and averaging 41.6 mm, while those taken in June ranged from 19 to 228 mm, averaging 134.7 mm. The 346 females collected displayed a similar size increase. March specimens ranged from 13 to 67 mm and averaged 40.0 mm, while those taken in June ranged from 21 to 197 mm, averaging 105.6 mm.

Penaeus setiferus was collected sporadically throughout the study with the numerical peak appearing in late June (Table 4). *P. setiferus* were, however, scarce in the two bays with only 10 specimens or about 3% of the total catch being taken. Specimens taken between February and May ranged in weight from 3.4 to 51 g and averaged 5.8 g, while those taken in June ranged from 0.2 to 6.6 g, averaging 0.7 g.

Callinectes similis was collected in May and June with the numerical peak appearing in late May (Table 4). This crab was taken throughout the study area but appeared to be least abundant in East Matagorda Bay. The width of 143 males ranged from 7 to 46 mm, averaging 24.1 mm, while that of 134 females ranged from 5 to 61 mm and averaged 20.9 mm.

TABLE 4

Number of specimens per try—net sample by date and habitat of selected species of invertebrates and vertebrates

Species	Area*	February 1	February 2	March 1	March 2	April 1	April 2	May 1	May 2	May 3	June 1	June 2	Cumulative total
Penaeus	I	0	0	0	0	0	1	3	28	109	79	78	298
aztecus	II	0	..	0	0	0	4	29	31	242	115	120	541
	III	..	..	0	0	0	1	3	28	95	15	25	167
	IV	..	..	0	0	1	26	72	51	159	61	67	437
Total		0	0	0	0	1	32	107	138	605	270	290	
Callinectes	I	1	0	4	0	17	13	25	5	1	1	4	71
sapidus	II	2	..	1	15	7	15	6	6	6	1	0	59
	III	..	..	0	1	10	9	8	15	10	6	9	68
	IV	..	..	6	23	15	6	7	7	4	2	2	72
Total		3	0	11	39	49	43	46	33	21	10	15	
Penaeus	I	1	0	1	0	5	1	2	3	1	0	43	57
setiferus	II	0	..	0	1	0	4	0	0	0	0	61	66
	III	..	..	0	0	0	0	1	1	0	0	0	2
	IV	..	..	0	0	0	0	0	0	0	0	2	2
Total		1	0	1	1	5	5	3	4	1	0	106	
Callinectes	I	0	0	0	0	0	0	13	7	7	2	5	34
similis ..	II	0	..	0	0	0	0	0	0	32	12	4	48
	III	..	..	0	0	0	0	4	0	30	2	1	37
	IV	..	..	0	0	0	0	0	1	3	1	1	6
Total		0	0	0	0	0	0	17	8	72	17	11	
Micropogon	I	9	10	13	7	64	78	29	12	17	8	9	256
undulatus	II	7	..	95	139	20	179	43	41	38	11	13	586
	III	..	..	17	2	94	127	95	54	53	28	9	479
	IV	..	..	40	388	79	121	225	112	89	61	39	1,154
Total		16	10	165	536	257	505	392	219	197	108	70	
Leiostomus	I	1	0	0	1	5	14	1	2	3	2	9	38
xanthurus	II	0	..	8	6	0	1	3	36	2	1	0	57
	III	..	..	6	24	14	0	5	5	0	11	14	79
	IV	..	..	33	2	33	88	103	57	30	25	43	414
Total		1	0	47	33	52	103	112	100	35	39	66	
Cynoscion	I	0	0	0	0	1	0	17	14	46	6	31	115
arenarius	II	0	..	0	0	0	1	2	6	12	5	10	36
	III	..	..	0	0	1	0	1	18	2	5	2	29
	IV	..	..	0	0	0	0	1	2	2	4	8	17
Total		0	0	0	0	2	1	21	40	62	20	51	

* Area I = Colorado River
II = Gulf Intracoastal Waterway
III = Matagorda Bay
IV = East Matagorda Bay
.. = No data

Vertebrates

Of the 39 vertebrate species taken in the try-net, 8 are considered as "common" and represent about 96.3 of the vertebrate catch (Table 3). Of these *Micropogon*

undulatus, *Leiostomus xanthurus* and *Cynoscion arenarius* are important to the sport and commercial fishery of Texas.

Micropogon undulatus was the most abundant species in the study area, accounting for about 39.2% of the entire try-net catch. The Atlantic croaker was taken from all habitats and catches were greatest in March and April (Table 4). Sizes increased gradually as the study progressed; specimens taken in February ranged from 14 to 137 mm and averaged 30.4 mm, while those taken in June ranged from 35 to 162 mm averaging 60.7 mm.

The second most abundant fish was *Leiostomus xanthurus* which was collected throughout the study period with the greatest catches made in early May (Table 4). About 77% of the total catch of the spot was taken from East Matagorda Bay. The size of this species increased gradually as the study progressed; specimens taken in February ranged from 13 to 42 mm and averaged 28.5 mm, while those taken in June ranged from 34 to 106 mm, averaging 51.0 mm.

Cynoscion arenarius was first caught in April and occurred throughout the study area until the end of June (Table 4). Sand seatrout were most abundant in late May and the greatest catches, made in the Colorado River, represented about 67% of the total catch for this species. The largest specimens, ranging from 41 to 192 mm and averaging 126.6 mm were taken in April, but smaller fish ranging from 22 to 73 mm and averaging 34.7 mm were collected during May and June.

DISCUSSION AND SUMMARY

The Colorado River-Matagorda Bay area has physical and biological features not unlike other estuarine areas on the upper Texas coast. Salinity ranges recorded during the study are similar to those recorded in 1962 for Galveston Bay by Stevens (1963), for San Antonio Bay by Childress (1963) and for Aransas Bay by Schultz (1963). Generally salinity ranged from less than 10‰ near sources of fresh-water discharge and often surpassed 30‰ near tidal passes.

Common invertebrates and vertebrates in the study area are representative of those found in other estuaries on the upper Texas coast. During 1962, personnel of the Texas Parks and Wildlife Department (formerly Texas Game and Fish Commission) found that commercial shrimp (*Penaeus spp.*), blue crabs (*Callinectes sapidus*), Atlantic croaker (*Micropogon undulatus*), spot (*Leiostomus xanthurus*), and sand seatrout (*Cynoscion arenarius*) were major faunal components of Galveston, San Antonio and Aransas Bays. The pinfish (*Lagodon rhomboides*), spotted seatrout (*Cynoscion nebulosus*), largescale menhaden (*Brevoortia patronus*), and bay anchovy (*Anchoa mitchilli*) have also been listed as major species within these bays. The relative numbers of these species vary during different seasons and years.

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TROPICAL AND TEMPERATE STRANDED SEEDS AND FRUITS FROM THE GULF OF MEXICO

Charles R. Gunn[1] and John V. Dennis[2]

ABSTRACT

Literature pertaining to buoyant tropical seeds and fruits (disseminules) seldom mentions the Gulf of Mexico. Yet some northern and western Gulf beaches regularly receive large numbers of tropical disseminules that have been carried by currents from the Caribbean region, northern South America, and Mexico. Frequent strandings coincide with onshore winds that move other tropical debris like *Sargassum* to shore. Padre Island, Texas beaches are especially rich in tropical disseminules. Other beaches which receive disseminules are located northward along the Texas coast, along the western coast of Louisiana, and on Santa Rosa Island, Florida. Disseminules of 34 tropical species and 24 temperate species have been collected from these beaches. Some of the temperate disseminules were carried by United States rivers into the Gulf currents and then stranded on Gulf Coast beaches.

INTRODUCTION

Published accounts of tropical seeds, or "sea beans" as they are usually called, reaching the coasts of Europe began to appear as early as 1570 (Pena and L'Obel, 1570). But not until the nineteenth century was it generally recognized that such seeds and other tropical debris were carried by the Gulf Stream from the Caribbean region to Europe. By 1950 several treatments dealt with ocean currents and stranded tropical seeds and fruits (disseminules), e.g., Guppy (1906, 1917), Colgan (1919), Ridley (1930), and Muir (1937). However, none discussed tropical disseminules in the Gulf of Mexico or the southeastern coast of Florida. Yet, from the Keys to Cape Kennedy tropical disseminules are often stranded from the nearby Gulf Stream.

Cross and Parks (1937) provide one of the first notes about tropical seed drift on Gulf Coast beaches. In their list of "Seaweed and Sea Drift" from beaches in the Corpus Christi region, they included *Cocos nucifera*, three species of *Cocos*, five species of seeds "evidently of the palm family," and nine species "representing beans and portions of pods." Eight common tropical drift disseminules were identified from beaches near Cameron, Louisiana by Fox (1944). Hildebrand and Gunter (1955), in a report on oil pollution along Gulf Coast beaches, listed a number of stranded disseminules, and they noted that most were stranded south of the mouth of the Colorado River, Texas, being rare elsewhere along the United States Gulf coast. Godfrey (1966) found three to four dozen sea hearts (*Entada*

[1] Botanist and Curator, Seed Collection, Plant Taxonomy Laboratory, Plant Genetics and Germplasm Institute, Agricultural Research Center West, ARS, USDA, Beltsville, Md. 20705.
[2] Freelance biologist, Princess Anne, Maryland.

gigas) on Padre Island beaches after a storm. Additional papers with collateral data are Arendt (1955), Dennis and Gunn (1972), Gunn (1968), and Gunn and Dennis (1971, 1972).

In her excellent book on sea shells of Texas, Andrews (1971) mentions a few disseminules and illustrates five of them. She also quotes and modifies Newcomb (1961) concerning an observation made by the shipwrecked explorer Cabeza de Vaca, who lived among the Karankawas from 1528 to 1538. The homeland of the Karankawas was from the west side of Galveston Bay to the southwest Corpus Christi Bay including the offshore islands, the coast, and a narrow strip of mainland. During the time he spent with the Karankawas, Cabeza de Vaca became a trader between the coastal Karankawas and Indian tribes of the interior. His original narrative was published in 1542 and an enlarged edition was issued in 1555. The latter edition was the original source of the English version which we

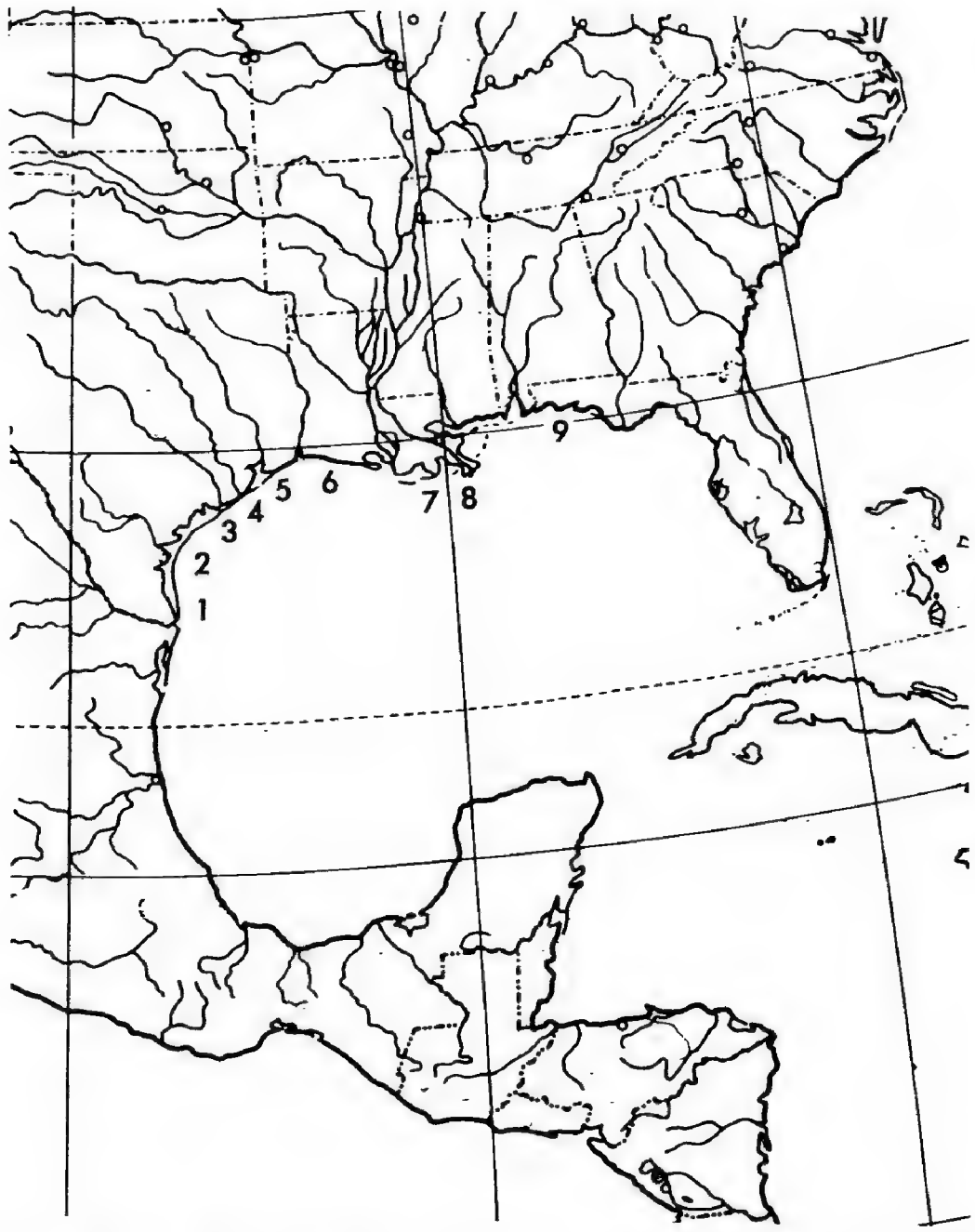

FIG. 1. Major collection sites along the Gulf coast. 1 = Brazos Island, Tex.; 2 = Padre Island, Tex.; 3 = Mustang Island, Tex.; 4 = Matagorda Peninsula, Tex.; 5 = High Island, Tex.; 6 = Holly Beach and Cameron, La.; 7 = Timbalier and Grand Islands, La.; 8 = Grand Terre Island, La.; and 9 = Santa Rosa Island, Fla.

consulted (Hodge, 1907). We have not seen the other English versions which are cited by Hodge in the introduction. The following is Hodge's report of the trading items listed by Cabeza de Vaca. "The principal wares were cones and other pieces of sea-snail, conches used for cutting, and fruit like a bean of the highest value among them [Karankawas], which they used as a medicine and employed in their dances and festivities. Among other matters were "sea-beads". Could the fruit-like bean or the sea-bead refer to a tropical stranded seed like *Entada gigas* or *Mucuna urens*? Newcomb does not speculate on the question except to observe that the bean probably is not a coral bean, *Erythrina*, because plants are found in the interior of Texas. Andrews believes that the passage refers to a "sea bean" and reports that she "has seen this distinctive bean in the herb sections of Indian markets throughout Mexico where its magical powers are still respected."

At this time we do not know if Cabeza de Vaca has published the first record of a tropical stranded disseminule on a temperate beach or not. We hope to clarify this point when all of the literature, including the original editions, have been located.

List from Gulf Coast Beaches

Disseminules of 58 species, 34 tropical and 24 temperate, have been identified from collections made by Dennis between 1960 and 1971, and by interested colleagues. Numbers following the species names in Table 1 are defined in the footnote and shown on the map in Fig. 1.

Seasonal Occurrence of Strandings

Beaches were usually visited during winter and spring months. Although almost no data exist for summer and fall, it is reasonable to believe that seasonal factors are important in the strandings of these disseminules. The first southeast winds during March and April bring tropical debris of all kinds, including seeds and fruits, to beaches from about Mustang Island southward. The appearance of *Sargassum* on these beaches has been correlated with southeasterly winds (Shelby, 1963).

Tropical disseminules were collected on Santa Rosa Island in western Florida in February and at several localities on the Louisiana coast in March. Visits to several of these localities in early winter were unproductive. Although we do not know enough about currents and weather patterns in the northern gulf, we suggest that a strong current flowing northward through the Straits of Yucatan and then northwest to the coast of Louisiana is responsible for the stranding of tropical disseminules from about the Mississippi Delta to the Texas coast (Fig. 2). In southeastern Florida, where, in contrast to the Gulf, a major tropical current passes close to the shoreline, strandings of tropical seeds can be expected during any season.

Sources of Disseminules

Disseminules of the 34 tropical species could have had their origin anywhere within the Caribbean region, Mexico and Central America, or perhaps in north-

TABLE 1

Tropical and temperate buoyant seeds and fruits collected along the United States portion of the Gulf of Mexico coast

Scientific name	Location number*	Source	
		Tropical	Local or northern
Acrocomia sp.	2, 3	x	.
Andira galeottina Standley	1	x	.
Andira inermis HBK.	2, 3	x	.
Astrocaryum sp.	2	x	.
Avicennia germinans (L.) L.	2, 3	.	x
Barringtonia asiatica (L.) Kurz	2	x	.
Bertholletia excelsa Humb. & Bonpl.	2	x	.
Caesalpinia borduc (L). Roxb.	2, 9	x	.
Calatola sp.	2	x	.
Calophyllum sp.	6	x	.
Canavalia rosea (Sw.) DC.	2, 6	.	x
Canna sp.	6	.	x
Carapa guianensis Aubl.	2	x	.
Carpinus caroliniana Walt.	7	.	x
Carya aquatica (Michx. f.) Nutt.	1, 2, 3, 5, 6, 7, 8, 9	.	x
Carya glabra Sweet	7	.	x
Carya illinoensis (Sarg.) K. Koch	1, 2, 3, 6, 7, 8	.	x
Carya sp.	2, 6, 7, 8	.	x
Chrysobalanus icaco L.	2	x	.
Cocos nucifera L.	2, 3, 6	x	
Corylus sp.	8	.	x
Crinum asiaticum L.	8	.	.
Dioclea reflexa Hook. f.	2, 6, 8	x	.
Dioclea sp.	2, 6	x	.
Elaeis guineenis Jacq.	1, 2, 3, 6	x	.
Entada gigas (L.) Fawcett & Rendle	2, 3, 4, 6, 7	x	.
Fevillea cordifolia L.	2, 8	x	.
Hernandia sp.	1, 2	x	.
Hippomane manchinella L.	2, 7, 8, 9	x	.
Ipomoea alba L.	2, 7	.	x
Ipomoea pes-caprae L.	6		x
Ipomoea sp.	2	.	x
Juglans cinerea L.	2, 5, 6, 8, 9		x
Juglans jamaicensis C. DC.	2, 8	x	.
Juglans nigra L.	2, 3, 6, 7, 8, 9	.	x
Machaerium lunatus (G.F.W. Meyer) Ducke	2	x	.
Manicaria saccifera Gaertn.	2, 3, 6, 8	x	.
Merremia discoidesperma ((Donn. Sm.) O'Donell	2, 6	x	.
Mucuna urens (L.) Medicus	2, 6, 8, 9	x	.
Mucuna sp.	2, 3, 4	x	.
Myristica fragrans Houtt.	2	x	.
Nyssa aquatica L.	2, 5	.	x
Omphalea diandra L.	2, 7	x	.
Orbigyna sp.	2	x	.
Platanus occidentalis L.	2, 3, 8	.	x

Scientific name	Location number*	Source	
		Tropical	Local or northern
Prunus sp.	7	.	x
Pterocarpus officinalis Jacq.	2, 8	x	.
Quercus lyrata Walt.	6, 7, 9	.	x
Quercus nigra L.	6, 7	.	x
Quercus sp.	3, 5, 6, 8	.	x
Rhizophora mangle L.	2, 4, 7	x	.
Sacoglottis amazonica Mart.	2, 6	x	.
Sapindus saponaria L.	2	.	x
Sideroxylon foetidissimum Jacq.	2	x	.
Sophora tomentosa L.	7	.	x
Spondias mombin L.	2, 8	x	.
Taxodium distichum (L.) Rich.	2, 5, 9	.	x
Terminalia catappa L.	2, 6, 7, 8	x	.

* 1. Brazos Island, Texas
2. Padre Island, Texas
3. Mustang Island, Texas
4. Matagorda Peninsula, Texas
5. High Island, Texas
6. Holly Beach, Louisiana
6. Cameron, Louisiana
7. Timbalier Island, Louisiana
7. Grand Island, Louisiana
8. Grand Terre Island, Louisiana
9. Santa Rosa Island, Florida

ern South America. Plants producing buoyant disseminules usually have a wide distribution; some are pantropical. In addition, several species that are predominantly tropical have ranges that extend northward along the Texas coast and in some cases into Louisiana. In this group are *Avicennia germinans*, *Canavalia*

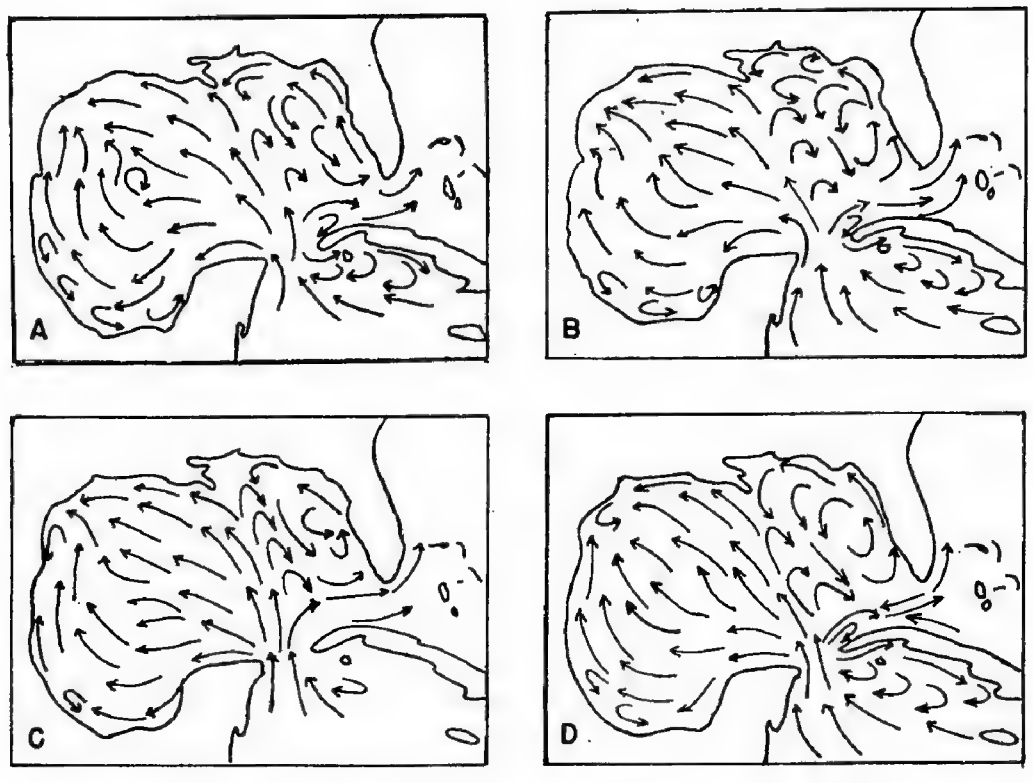

FIG. 2. Surface currents in the Gulf of Mexico. A = Autumn (Oct., Nov., Dec.); B = Winter (Jan., Feb., Mar.); C = Spring (Apr., May, June), and D = Summer (Jul., Aug., Sep.). (Redrawn from United States Navy, 1965).

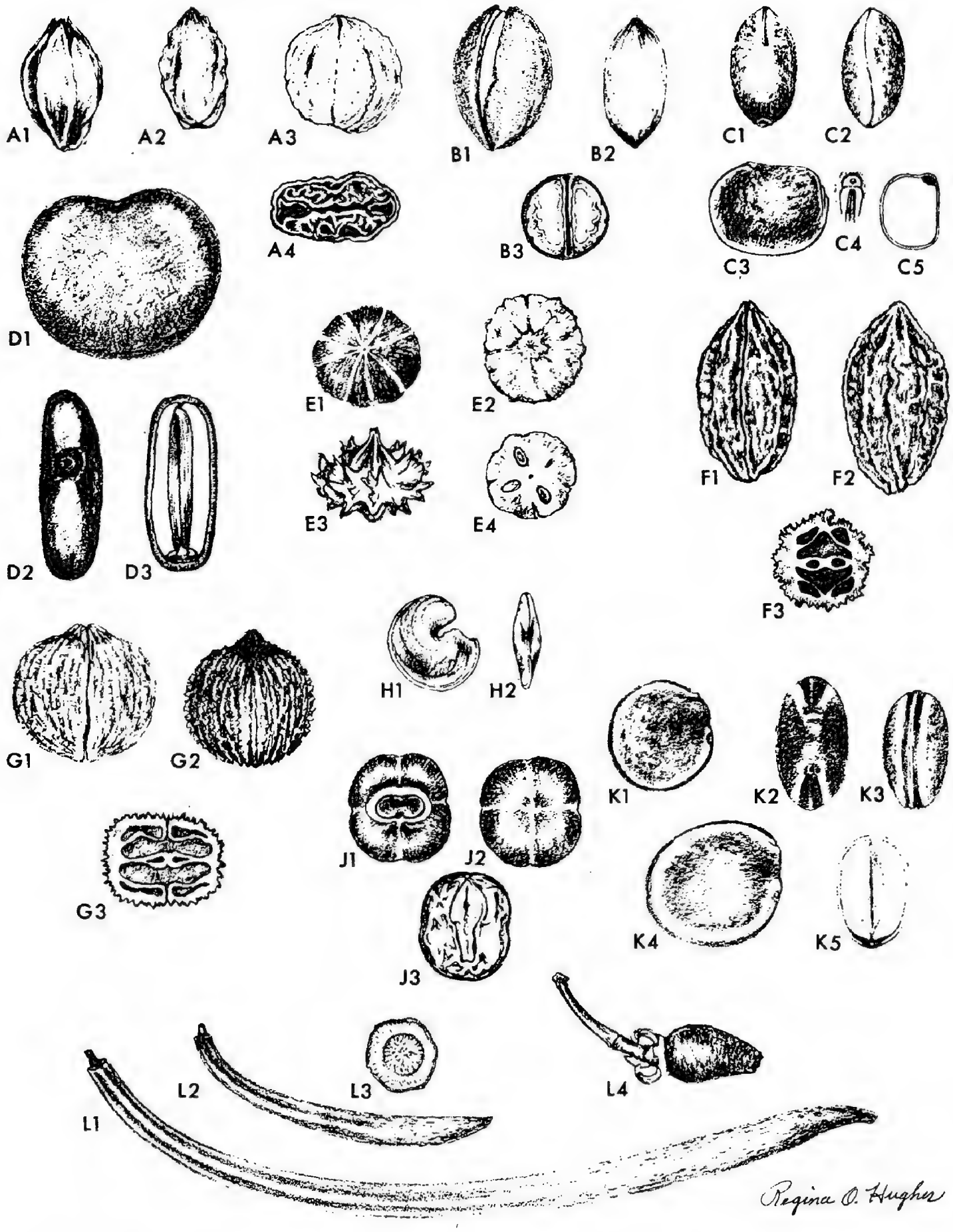

FIG. 3. A selection of tropical and temperate disseminules collected along beaches of the Gulf of Mexico: *Carya aquatica* (Michx.) Nutt. A 1–4, *C. illinoensis* (Sarg.) K. Koch B 1–3, *Dioclea reflexa* Hook. f. C 1–5, *Entada gigas* (L.) Fawcett & Rendle D 1–3, *Hippomane mancinella* L. E. 1–4, *Juglans cinerea* L. F 1–3, *J. nigra* L. G 1–3, *Machaerium lunatus* (G. F. W. Meyer) Ducke H 1–2, *Merremia discoidesperma* (Donn. Sm.) O'Donell J 1–3, *Mucuna urens* (L.) Medicus K 1–4, *Rhizophora mangle* L. L 1–4. A1, entire fruit; A2, endocarp, side view; A3, endocarp, face view; A4, endocarp, cross section; B1, entire fruit; B2, endocarp; B3, endocarp, cross section; C1, seed, lateral view; C2, seed, hilum view; C3, seed, face view; C4, detail of micropyle; C5, seed,

rosea, Ipomoea alba, I. pes-caprae, and *Sophora tomentosa.* Disseminules from any of these five species could either be of local origin or be brought by currents from the tropics. Similarly the pecan, *Carya illinoensis* (Fig. 3, B 1–3) may be of local or tropical origin, or be brought to the Gulf by southern flowing United States rivers.

The red mangrove (*Rhizophora mangle*) (Fig. 3, L 1–4) is found on the Mexican coast to a point just south of the Texas border and on the west coast of Florida as far north as Hillsborough County. An isolated colony is present in Levy County, Florida. Correll and Johnston (1970) observed that red mangrove seedlings "are commonly washed ashore (especially near the mouth of the Rio Grande), where they have been known to sprout, but no living plant has apparently thus far become established in Texas." Although red mangrove seedlings washed ashore in large numbers on Timbalier Island, Louisiana (Hildebrand and Gunter, 1955), the tree has not become established in Louisiana.

Two tropical species have predominantly South American ranges. *Sacoglottis amazonica* and *Manicaria saccifera* range from the Amazon estuary northward along the coastline to Costa Rica. Fruits of both species (Fig. 4, A-I) have commonly been found on several Gulf Coast beaches.

With two exceptions, all of the tropical disseminules listed in Table 1 as coming from Gulf beaches have also been found on beaches of southeastern Florida. The two exceptions are fruits of *Machaerium lunatus* (Fig. 3, H 1–2) and *Andira galeottina,* woody legumes growing from Mexico southward. Dennis collected several fruits of *A. galeottina* in the drift along the coast of Veracruz, Mexico. There is no mention of *A. galeottina* in any of the literature pertaining to stranded disseminules.

Only one species, butternut (*Juglans cinerea*) (Fig. 3, F 1–3), is completely northern in origin. It is found in the central Mississippi valley (essentially north of the southern Tennessee border) northward into Canada. Butternut endocarps could reach the Gulf and southeastern Florida beaches by water only after floating down rivers like the Mississippi and being carried by ocean currents to the beaches. The southernmost beach which yielded butternut endocarps was one near the northern end of the National Seashore on Padre Island, Texas. A few butternut endocarps have been found on beaches of southeastern Florida. Black walnut (*J. nigra*) (Fig. 3, G 1–3), whose natural range comes within a few miles of the coast produces endocarps that may be carried long distances by rivers and ocean currents. Ten endocarps were found on a beach at the north end of the National Seashore on Padre Island, 22 and 23 March, 1971. The closest source would be southeastern Texas. However, rivers entering the northern Gulf along the Louisiana coast are another and more likely source (Fig. 1).

In addition to butternut and black walnut endocarps, endocarps of water

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cross section; D1, seed, face view; D2, seed, hilum view; D3, seed, cross section; E1, entire fruit; E2, fruit without exocarp; E3, weathered fruit; E4, fruit, cross section; F1, entire fruit; F2, endocarp; F3, endocarp, cross section; G1–2, endocarps; G3, endocarp, cross section; H1, seed, face view; H2, seed, lateral view; J1, seed, hilum view; J2, seed, ventral view; J3, seed, cross section; K1 & 4, seed, face view; K2 & 3, seed lateral view; K5, seed, cross section; L1, average size seedling; L2, small seedling; L3, seedling, cross section; L4, fruit (x0.5).

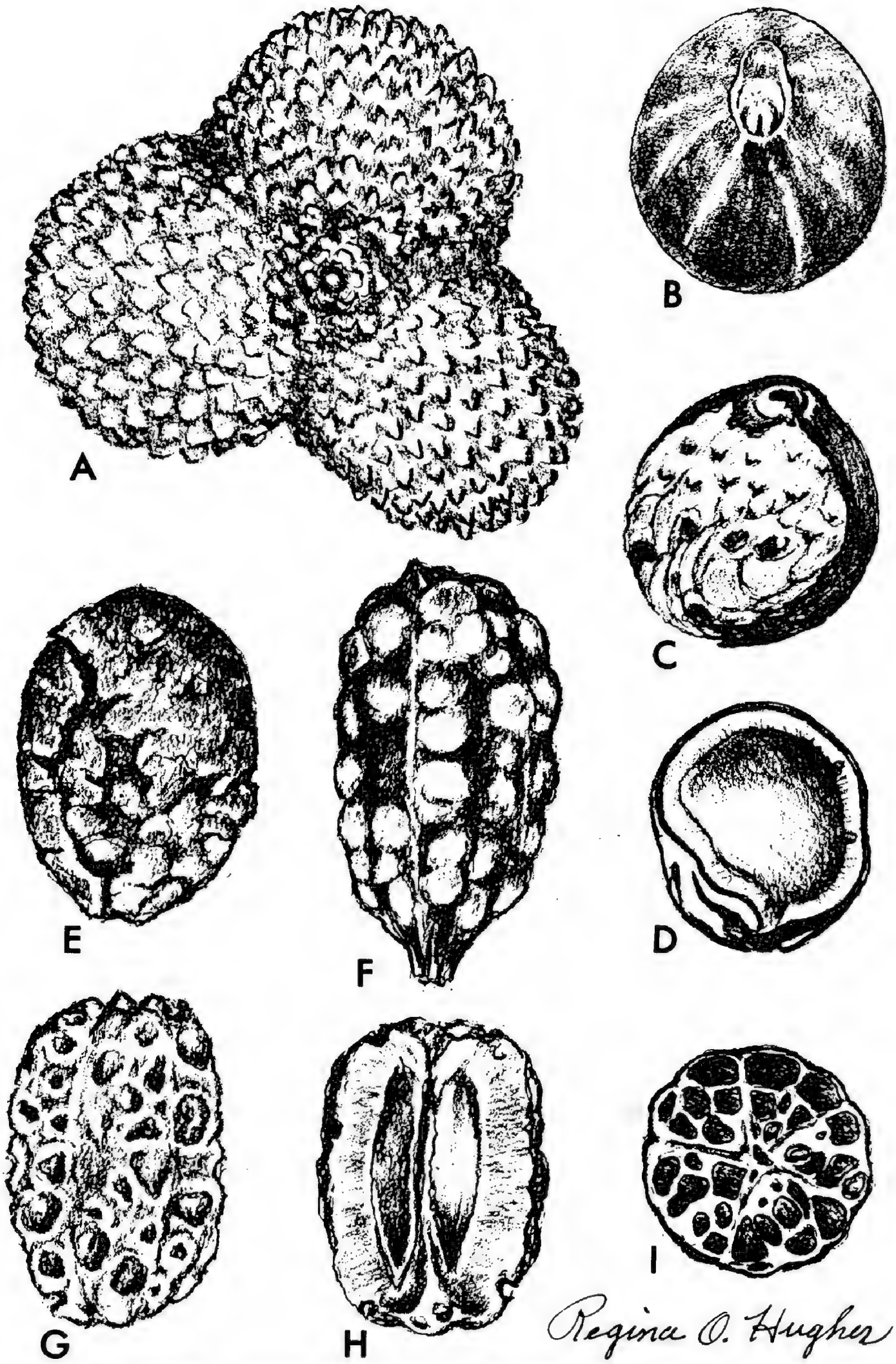

FIG. 4. Two tropical disseminules collected along beaches of the Gulf of Mexico: *Manicaria saccifera* Gaertn. A-D, and *Sacoglottis amazonia Mart.* E-I. A, 3-seeded fruit (1- and 2-seeded fruits may be found); B, endocarp; C, partially eroded endocarp; D, endocarp, cross section revealing hollow seed; E, entire fruit; F, fruit without exocarp; G, weathered fruit; H, fruit, longitudinal section; I. fruit, cross section (x1).

hickory (*Carya aquatica*) and pecan (*C. illinoensis*) (Fig. 3 A 1–4 & B 1–3) occur more frequently on Gulf coast beaches than they do on southeastern Florida beaches. This is due to the influx of temperate debris brought to the Gulf by south flowing rivers, especially the Mississippi River.

DISCUSSION

Disseminules reaching beaches of the Gulf of Mexico have diverse origins (United States, Mexico, Caribbean region, Central America, and northeastern South America) and represent 28 families. Based on data gathered from disseminules collected along the beaches of southeastern Florida during 1971 and 1972, and our observations of disseminules from Gulf coast beaches, we believe that most of these Gulf disseminules were stranded in a viable condition. Viability of the Florida seeds was determined by using 2,3,5-triphenyl tetrazolium chloride. Based on our extensive field observations we believe that freezing prevents many, e.g., *Barringtonia*, *Dioclea*, *Entada*, *Merremia*, *Mucuna*, and *Sacoglottis*, from becoming established on the northern Gulf coast. Other disseminules such as butternut, black walnut, and palm endocarps usually are stranded with dead seeds. Some of the palms may have empty seed cavities.

One of the more interesting seeds, collected by Jerry Walls from Grande Terre Island, Louisiana during March, 1971, is *Crinum asiaticum* (Fig. 5). These tuber-like seeds had sprouted when they arrived in Maryland a month later. It is not unusual for these seeds to sprout and for the seedlings to remain alive for months without being planted.

Tropical disseminules are unreported from long stretches of Gulf coast beaches. Examples of unproductive coastlines where there has been some field work are

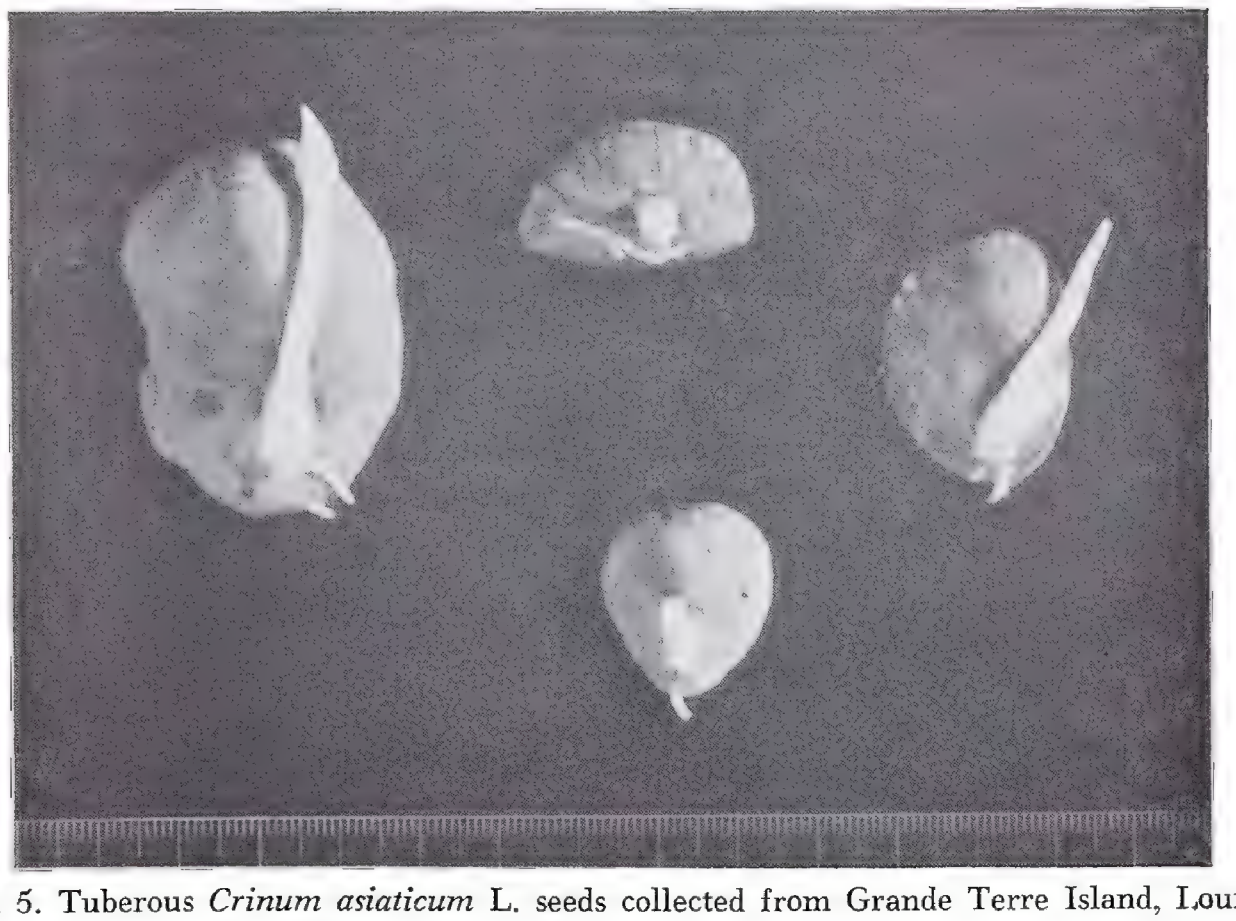

FIG. 5. Tuberous *Crinum asiaticum* L. seeds collected from Grande Terre Island, Louisiana sprouted while enroute to Maryland.

the east coast of Texas from Galveston Bay to Sabine Pass, and the west coast of the Florida peninsula. Both coastlines receive non-tropical disseminules, and the west coast of Florida also receives such semitropical species that grow locally as red and black mangrove. Whether more intensive field work would reveal strandings on these coastlines, we do not know. It would appear however, that some coasts are much more favorably situated than others in regard to stranding of tropical disseminules of distant origin. Also it should be borne in mind that under some conditions, disseminules are quickly buried by sand and therefore are not evident to the collector. Currents and seasonal weather factors must play decisive roles in where these disseminules are deposited. This is an area where oceanographers and botanists could cooperate to mutual advantage. Also, almost nothing is known of the distribution and occurrence of tropical disseminules at sea. Whether working in the Gulf of Mexico or any other body of water, oceanographers could be of invaluable service if they would report and save any disseminules that they catch in plankton nets or other devices. If they would report the location, numbers observed, how deep in the water the disseminules were floating, and similar details, we would have data that, to our knowledge, have never before been recorded.

ACKNOWLEDGMENTS

We are indebted to Clair A. Brown for collections sent to us from Grand Isle and Cameron, Louisiana; to Jerry G. Walls for a collection from Grand Terre Island, Louisiana; to Regina O. Hughes who prepared the disseminule drawings; and to the Botany Department, Smithsonian Institution for supporting this research.

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CORPUS CHRISTI PASS: A HURRICANE MODIFIED TIDAL INLET ON MUSTANG ISLAND, TEXAS[1]

Richard A. Davis, Jr., W. George Fingleton, Gerald R. Allen, Jr., Charles D. Crealese, William M. Johanns, Joseph A. O'Sullivan, Catherine L. Reive, Sandra J. Scheetz and Gary L. Stranaly

Department of Geology, Western Michigan University, Kalamazoo, Michigan 49001

ABSTRACT

Corpus Christi Pass, near the southwestern end of Mustang Island, represents a typical hurricane modified tidal inlet. During the time between severe storms the pass is closed at its seaward end by sediment provided by littoral drift. Such was the case between Hurricane Carla (1961) and Hurricane Beulah (1967). The pass has been open since the latter storm but is presently almost filled with sediment.

Both ebb and flood deltas are present; however, the ebb delta is poorly developed because of the wave dominated nature of the coast and the flood dominance of the tides in the pass. Flood currents reach near a meter/sec., whereas ebb currents are typically only about 0.2 meters/sec. Bed forms are dominated by ripples and reflect the flood dominance.

INTRODUCTION

The barrier island system of the Texas coast extends for a few hundred kilometers, being absent only near the deltaic plains of the Sabine, Brazos and Colorado Rivers. Throughout this barrier island system there are a number of passes or inlets which interrupt its continuity. Such passes fall into three categories: natural inlets, natural inlets later modified and structured by man, and those passes which were dredged and in some cases also structured by man. Within the category of natural breaks in the barrier island there are two possible origins; those inlets which are the result of large tidal exchange and those resulting from a breaching of the island during a hurricane. The passes at Galveston, San Luis Pass, and Aransas Pass are examples of tidal formed features although both Galveston and Aransas have been subsequently modified by man. Corpus Christi Pass is somewhat complex in that it is periodically regenerated by hurricanes, but it is part of a natural tidal inlet system including two other major channels, Newport Pass, and Packery Channel.

Although hurricane passes are rather shallow and generally not navigable, they are of considerable significance in the overall coastal environment scheme. A large amount of water is exchanged between the open ocean and the coastal bays.

[1] Data for this paper were collected as a group project by the Coastal Sedimentation class of Western Michigan University, Spring 1972, under the direction of the senior author. All co-authors shared equally in data collection; the manuscript and figures were prepared by Davis.

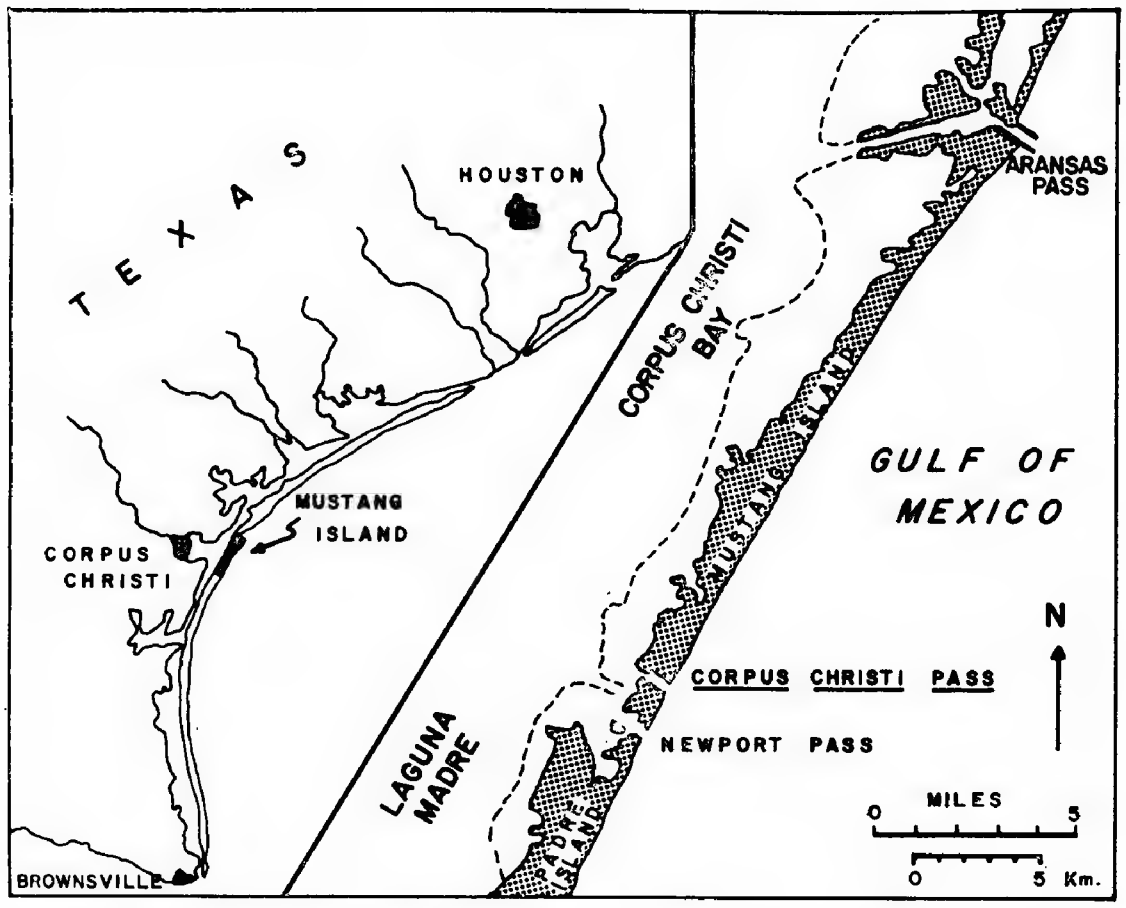

FIG. 1. Index map of Mustang Island, Texas, showing location of Corpus Christi Pass.

This may aid in migration of marine organisms, provide a food source for organisms, and help to achieve a desirable water chemistry in the bays.

Some detailed studies of inlets on the eastern coast of Texas have recently been completed at Rollover Pass (R. M. Sorenson, personal communication), a dredged inlet, and at Brown Cedar Cut (Mason and Sorenson, 1971; Piety, 1972), a natural inlet later modified by man. Andrews (1970) studied a large hurricane generated washover fan associated with Cedar Bayou, a natural pass on St. Joseph Island. The present study represents an attempt at examining the characteristics of a natural hurricane modified pass along the Texas Coast. Corpus Christi Pass is located near the southeastern end of Mustang Island, Texas, (Fig. 1), and is immediately north of Newport Pass, a similar feature. The pass is approximately a half kilometer wide and nearly two kilometers long. The only appreciable affect of man in the pass itself is a bridge which crosses the pass near the center and causes a constriction in the pass width. Field data for this discussion were collected over a ten day period during May, 1972.

STORM GENERATED CHANGES

During the approach of a hurricane there is a significant storm tide associated with the usual large waves. If the storm is intense and moves slowly, the storm tide could reach three or more meters. The strong onshore winds and storm tides force much water to pile up in the coastal bays. After the storm proceeds over the barrier island there is a great flushing of this water from the bays. As this takes place, much sediment is excavated from the passes leaving a rather straight and relatively deep channel (Fig. 2).

FIG. 2. (a) Corpus Christi Pass as it was in June, 1967 prior to Hurricane Beulah (photo courtesy of E. W. Behrens). (b) After Hurricane Beulah (October, 1967) the pass was opened in the form of a rather straight channel. Note that the bridge was washed out (photo courtesy of E. W. Behrens).

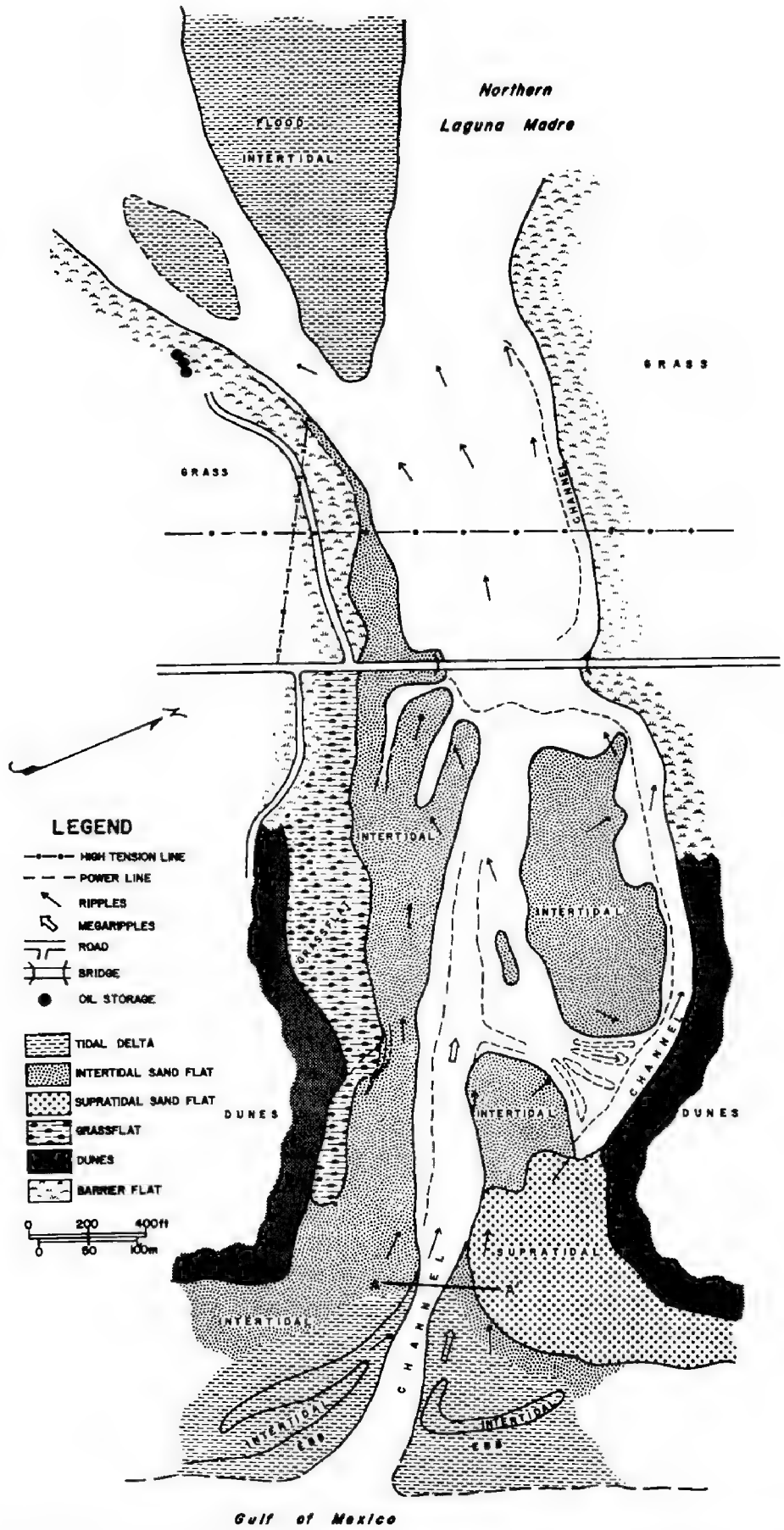

FIG. 3. Map of Corpus Christi Pass showing various environments which comprise the pass and adjacent vicinity. Flood oriented bedforms are also indicated.

Even though Corpus Christi Pass is a rather large natural pass and can carry much water during the tidal cycle, it may be a short lived feature. Littoral drift may be rather rapid along the barrier coast and much sediment can be transported in a short time. For example, prior to Hurricane Carla in 1961, Corpus Christi Pass was closed along the Gulf beach side of Mustang Island. Carla, which

was an extremely severe hurricane, opened the pass. In a few years the littoral drift closed it again (Fig. 2a) and Hurricane Beulah reopened it in 1967 (Fig. 2b). Since that time the pass has remained open with much tidal exchange, however it will likely close again.

MORPHOLOGY

A detailed survey was made of the entire Corpus Christi Pass area in order to construct a map showing various features associated with the pass (Fig. 3). The pass contains a complex arrangement of channels, intertidal sand bars and flats, and tidal deltas. Current ripples are nearly ubiquitous and with rare exception are the only bed forms present.

Tidal Deltas

Both ebb and flood deltas are present in Corpus Christi Pass (Fig. 3), however there is considerable difference in their size and shape. The ebb delta on the Gulf side of the pass is quite small and is considerably modified by wave action.

The ebb delta is nearly symmetrical with a slight displacement to the southeast. Its seaward limit is essentially parallel to the adjacent beach, however there is a slight convex-seaward configuration as evidenced by the rows of breakers. Only one channel crosses the ebb delta and small arcuate ebb shields (Hayes, *et al.*, 1969) protect the ebb delta. These features are the topographic highs on the ebb delta located on either side of the channel (Fig. 3). In contrast, the flood delta is quite large and extends considerably beyond the mouth of the pass into the northern end of Laguna Madre. The broad flat flood delta is largely intertidal with a few small, vegetated, supratidal islands.

Sand Flats

The bulk of the pass area on the seaward side of the highway bridge is comprised of broad sand flats with one main channel (Fig. 3). Nearly all of these sand flat areas are exposed during low tide. A broad supratidal flat which is actually an incipient spit, is present on the northeast corner of the Gulf side. The intertidal flats are mostly rippled and are burrowed by crabs and shrimp.

The bay side of the pass is essentially one, broad sand flat with the exception of the deep channel on the north side. This area is all subtidal and is covered by a meter or more of water in most places.

Channels

The main channel nearly bisects the pass through the ebb delta and for a few hundred meters beyond (Fig. 3). At this point the channel widens, becomes shallow, and bifurcates. A shallow and broad channel, less than a meter deep at low tide, continues toward the bridge and another shallow channel turns sharply toward the northeast, eventually spilling into the deep channel along the north edge of the pass.

The deep channel begins abruptly behind the supratidal sand flat with its

southeasternmost portion containing stagnant water. This channel is 2 meters deep and its actively eroding dunes and back-island areas along its steep northern bank. As the channel approaches the highway bridge it is diverted toward the south by the artificial fill associated with the bridge. Beneath the bridge in the constricted part of the pass the channel reaches its maximum depth of 4 meters. Beyond the bridge the deep channel continues along the northeast side of the pass (Fig. 3) where it retains the character of the channel. On the flood delta the channel begins to shallow and lose its definition.

BEDFORMS

Tidal passes typically are covered with various bedforms which owe their nature to their specific location, depth of water and tidal current velocity within the pass. The tidal pass acts essentially like a river and the bedforms generated are much like the typical fluvial forms. By contrast however, tidal passes alternately flow in opposite directions as the tide reverses. As a result, the bedforms may present a rather complicated pattern with ebb oriented forms dominating at some locations and flood oriented at others. The University of Massachusetts, Coastal Research Group (Hayes, *et al.*, 1969) has made numerous studies of such bedforms in New England estuaries.

Corpus Christi Pass is a low energy tidal pass because of the low tidal range and small quantity of water that is carried relative to large estuaries on tide dominated coasts. The bedforms present reflect this condition. During flood tides, which dominate the pass, ripples are present throughout the pass with few exceptions. Megaripples (wave length between 0.6 and 6.0 meters) were found at two locations: behind the ebb delta shield and also in the main channel near the area of bifurcation (Fig. 3). Those located behind the ebb shield were about one meter in wave length and regular in shape, whereas scour megaripples were present at the other location. The latter were about three meters in length with a height of about 0.3 meters.

Ripples covered all of the remaining portion of the pass except for the supratidal flats. Throughout the pass there was a general uniformity in the ripples. They were straight and fairly continuous with wave lengths from 12 to 20 cm. Orientation of the ripples during flood tide showed the expected pattern relative to the morphology of the pass; ripples were oriented with the channels and the slope of the sand flats (Fig. 3). Those ripples which deviated markedly from this orientation were oriented toward the deep channel on the northeast side of the pass and were essentially normal to it. From the bridge to Laguna Madre the ripples were oriented essentially as expected, parallel to the pass margins.

Bedforms reflect the unusual character of the tides in that nearly all ripples are flood oriented, even during ebb tides. In the channels where currents are swiftest, ripples are ebb oriented, however no megaripples are generated during ebbing tides.

HYDROGRAPHY AND SEDIMENTATION

Mean tide range along Mustang Island is about 0.5 meters. Although this is a

small range, there is still a fairly large amount of water which passes through its channel with a maximum of 45 cubic meters/sec. under normal conditions. The most obvious factor contributing to the pronounced tidal asymmetry of the pass is the wind tide component. Winds along this portion of coast are generally onshore and biomodal from the southeast and northeast (Lohse, 1955). Recent studies have shown that during two month-long periods, the onshore wind tide was present for nearly 85 percent of the time with the magnitude near 0.3 meters (Davis and Fox, 1972). As a result, the wind tides may represent a sizeable portion of the total tidal range. This gives rise to flood tides which have a longer duration and faster flow than the ebb tides. Flood tidal currents commonly reached velocities of 55 cm/sec., whereas ebb tides had a maximum velocity of 25 cm/sec. during the study period.

Ebb tides are only of near equal or greater significance than flood tides when onshore wind tides are absent and particularly after the passage of cold fronts ("northers") during winter. These fronts bring strong offshore winds which commonly blow water out of the shallow bays causing unusually swift ebb currents. The above is based on only general observations during the winter of 1972, no actual current measurements were made.

Another tidal "oddity" that may be related to the tidal character of Corpus Christi Pass is the overwhelming ebb dominance of Aransas Pass, located about 17 kilometers northeast. This is the major tidal channel along the central Texas barrier island coast. It is near a kilometer wide and dredged to 13 meters. Ebb currents during spring tides and especially after "northers", may exceed 2 meters/sec. It is possible that Corpus Christi Pass and the adjacent Newport Pass (Fig. 4) together with Aransas Pass form some type of tidal circulation cell with a clockwise motion.

Post-hurricane Recovery

There is a general pattern to the changes that take place in tidal pass morphology after they are opened by hurricane conditions. Immediately after passage of Hurricane Beulah in September of 1967, Corpus Christi Pass was essentially straight with no apparent sand bodies in the pass (Fig. 2b). As time proceeds, a slight spit develops on the northeast side of the northeast side of the pass mouth. Prevailing flood tide currents carry some of the spit sediment into the pass. Some of this sand fills the pass in the form of intertidal sand flats and the rest is added to the large flood delta. As the pass becomes choked with sediment the narrow and deep channel forms on the northeast side of the pass (Fig. 4). Its deep nature and position reflect the Coriolis effect and the flood dominance of tides. A pronounced similarity exists between Corpus Christi and Newport passes during this recovery period (Fig. 4).

Nearly all of the shallow sand flats are located seaward of the highway bridge (Fig. 3). There is a slow progradation of sediment as sediment is carried over the shallow flats and cascades down the steep slip face of the sand body and into the very deep and swift moving water of the channel. The sediment is then carried toward the flood delta.

FIG. 4. Oblique photos showing the marked similarity between (a) Corpus Christi Pass and (b) Newport Pass located about 2 kilometers to the south.

SUMMARY

Corpus Christi Pass is a rather typical example of a hurricane modified tidal pass in the Texas barrier island complex. Prolonged periods without hurricanes

or intense tropical storms permit littoral transport of sediment to close the pass at its seaward opening. While tidal exchange is operating through the pass there is a distinct flood dominance. This is due largely to onshore wind tides which reinforce flood currents and produce a distinct tidal velocity asymmetry. Ripples dominate the surface structures and show flood orientation even during most ebb flow conditions.

ACKNOWLEDGMENTS

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A KEY TO UNBRANCHED, CYLINDRICAL BROWN ALGAE

Michael J. Wynne

The Department of Botany, The University of Texas at Austin

ABSTRACT

A list has been compiled of 40 species of phaeophycean algae possessing unbranched, cylindrical thalli. A diagnostic key is presented in order to facilitate the recognition of these superficially similar brown algae. Data on geographical distribution and references to more complete descriptions and illustrations of these algae are also included.

INTRODUCTION

A disconcertingly large number of brown algae present a superficially similar thallus form, namely, that of an unbranched cylinder. The objective of this paper is to compare these algae on a worldwide basis and to arrange a method to expedite their identification. This account is restricted to those simple brown algae of relatively macroscopic size (at least 1 cm in length).

DISCUSSION OF THE KEY

The Key has been prepared with an effort made at avoiding the use of dimensions (as length and width of thalli) as far as possible, since such characteristics depend on the age of the plant and thus tend to be quite variable and unstable. Anatomical traits, involving methods of growth, reproductive structures, and shape of assimilatory filaments or paraphyses, have been incorporated into the Key. These criteria are generally more constant in making reliable identifications.

The first pair of alternatives in the Key presents perhaps the most fundamental criterion for distinguishing the brown algae, i.e., parenchymatous vs. non-parenchymatous construction of the thallus. In such genera as *Litosiphon*, *Scytosiphon*, *Stictyosiphon*, and *Dictyosiphon* the presence of both transverse and longitudinal divisions making up the parenchyma is easily observed. In other genera such as *Cladosiphon*, *Saundersella*, *Myriogloia*, and *Sauvageaugloia* the non-parenchymatous nature of the thalli is also easily detected when one sections a thallus and sees the loose arrangement of uniseriate, branched filaments, usually held together merely by mucilage.

However, the anatomy of certain genera is not so readily determined. Thalli of *Chordaria*, *Myelophycus*, *Pseudochorda*, and *Analipus* have a compact organization, with a multiaxial system producing a pseudoparenchymatous tissue. Longitudinal sections in the apical regions should reveal the presence of a sub-

apical meristem consisting of several central filaments and the absence of longitudinal divisions. The multicellular, uniseriate assimilatory filaments of these genera will also aid in indicating their affinities with the non-parenchymatous Chordariales rather than the parenchymatous Dictyosiphonales. Thalli of *Chorda* and *Halosiphon* have a parenchymatous construction, although mucilage is produced which typically separates the filaments of the medulla, resulting in a perhaps pseudoparenchymatous appearance. The unicellular paraphyses of these two genera should serve as a means to separate them from the above chordarialean genera.

1a. Thallus constructed[1] by both longitudinal and transverse divisions of cells (i.e., truly parenchymatous) 2
1b. Thallus constructed[1] by monosiphonous filaments interwoven together at maturity 23
2a. Thallus clavate, saccate, with an inflated, hollow distal portion and a gradually tapering stipe 3
2b. Thallus uniformly cyclindrical, solid or hollow at maturity 5
3a. Single chromatophore per cell; only plurilocular sporangia present ..... *Utriculidium durvillei*
3b. Numerous chromatophores per cell; unilocular sporangia present 4
4a. Both unilocular and plurilocular sporangia present on the macroscopic plant; unilocular sporangia sunken rather than protruding; hairs or paraphyses absent; thallus simple or at times proliferous ..... *Corycus lanceolatus*
4b. Only unilocular sporangia present on the macroscopic plant; pyriform unilocular sporangia situated among paraphyses; tufts of hairs arising from cryptostomata; thallus always simple ..... *Adenocystis utricularis*
5a. Thallus frequently with constrictions at intervals 6
5b. Thallus wihout conspicuous constrictions 7
6a. Noticeable patches, or sori, of unilocular sporangia scattered over thallus surface; cells each with numerous chloroplasts ..... *Asperococcus* (in part)
6b. Thallus surface becoming uniformly covered with plurilocular sporangia at maturity; cells each with a single chloroplast..... *Scytosiphon* (in part)
7a. Thallus length of sublittoral plants exceeding 50 cm (may attain 1–5 m); littoral specimens shorter 8
7b. Length of thallus more restricted, less than 30 cm 11
8a. Thallus solid or hollow, when hollow the central cavity interrupted by diaphragms; unicellular paraphyses with flattened tops; true colorless hairs with basal meristems present 9
8b. Thallus solid or hollow, when hollow the central cavity without diaphragms; unicellular paraphyses with round tops; true colorless

[1] Consult the previous paragraph to be aware of possible difficulties with pseudoparenchymatous genera such as *Chordaria, Pseudochorda, Myelophycus*, and *Analipus.*

hairs with basal meristems absent and replaced by assimilatory filaments to 10 mm long, with basal meristem but borne on a short stalk that is not shed with the filament 10

9a. Thallus with delicate deciduous hairs only ..... *Chorda filum*

9b. Thallus covered by multicellular filaments bearing numerous chromatophores ..... *Chorda tomentosa*

10a. Thallus dark brown to almost black; paraphyses to 200μ long, extending beyond the sporangia ..... *Halosiphon tomentosus*

10b. Thallus yellow to yellowish-brown; paraphyses 75–100μ long, equal to or shorter than sporangia in length; texture looser than in *H. tomentosus* ..... *Halosiphon altae*

11a. Outermost cells of cortex extremely large (utricle-like) relative to subcortical cells and larger than the unilocular or plurilocular organs which may be present ..... *Delamarea attenuta*

11b. Outermost cell of cortex small relative to subcortical cells, with cells progressively larger toward medulla 12

12a. Growth initially uniseriate, only gradually becoming parenchymatous; thallus usually solid, but may become hollow below 13

12b. Growth parenchymatous very early in development; uniseriate portions not evident; thallus typically hollow 17

13a. Distinct annular zones of sporangia present ..... *Protasperococcus myriotrichiiformis*

13b. Distinct annular zones of sporangia lacking; sporangia randomly distributed 14

14a. Plurilocular sporangia clearly emergent ..... *Asperococcus scaber.*

14b. Plurilocular sporangia nearly immersed 15

15a. Plants tending to occur singly, never in large tufts; simple or sparingly branched ..... *Stictyosiphon subsimplex*

15b. Plants gregarious, in conspicuous tufts; individual thalli always unbranched 16

16a. Length of thalli 1–3 cm; hairs absent ..... *Litosiphon filiformis*

12b. Length of thalli 5–10 cm; hairs preesnt ..... *Litosiphon pusillus*

17a. Thallus bearing plurilocular sporangia, which occur in indefinite superficial sori 18

17b. Thallus bearing unilocular sporangia 20

18a. Both plurilocular and unilocular sporangiate thalli occur; distinctive unicellular paraphyses absent; true hairs absent ..... *Melanosiphon intestinalis* (in part).

18b. Only plurilocular sporangiate thalli occur; distinctive unicellular paraphyses may be present, scattered among the plurilocular sporangia; true hairs, often in tufts, present 19

19a. Basal system limited to a small discoid holdfast, with one to many erect thalli ..... *Scytosiphon* (in part).

19b. Well developed basal system, with several cylindrical thalli ..... *Colpomenia sinuosa* f. *deformans* sensu S. & G. (1924).

20a. Only unilocular sporangia present, sunken in the cortical tissue 21

20b. Both unilocular and plurilocular sporangia present; the unilocular sporangia protruding and situated among multicellular filaments.....22
21a. Shoot apex in the process of growth with transversely dividing apical cell; plants small 2–5 (–8) cm tall and rarely reaching 1 mm in diam.; simple or sparingly branched .....*Dictyosiphon ekmani*
21b. Growth in length by intercalary cell divisions; plants larger, 10–40 (–80) cm tall and more than 1 mm in diam. (2–8); always simple..... ..... *Coilodesme cystoserirae*
22a. Single chromatophore per cell; both unilocular and plurilocular sporangiate plants may occur (with a given plant bearing only one type or reproductive organ); unilocular sporangiate plants with assimilatory filaments, which may be biseriate in portions; plurilocular sporangia uniseriate, arranged in compact rows, and forming large patches .....*Melanosiphon intestinalis* (in part).
22b. Numerous chromatophore per cell; both kinds of reproductive organs may occur on the same plants; assimilatory filaments are multicellular and always uniseriate; plurilocular sporangia are ovoid, pod-shaped, and stalked .....*Asperococcus* (in part).
23a. Apex terminated by a conspicuous tuft or crown of filaments.....24
23b. Apex not terminated by a conspicuous tuft or crown of filaments.....25
24a. Thallus club-shaped with an enlarged distal portion .... *Tomaculopsis herbertiana*
24b. Thallus uniformly cylindrical throughout, except for point of attachment .....*Bellotia simplex*
25a. Growth by means of a single apical cell .....*Nemacystus subsimplex*
25b. Growth by means of intercalary transverse divisions of several filaments 26
26a. Central filaments sympodially constructed (i.e., growing points being continually deflected to the side, with laterals temporarily assuming responsibility for growth in length) 27
26b. Central filaments monopodially constructed (i.e., the filaments responsible for growth in length are not replaced by their lateral filaments) 29
27a. Central axis more or less hollow; outer parts with more or less parenchymatous cells sealed together 28
27b. Central axis not hollow .....*Suringaria harveyana*
28a. Outer cells 4–8 times as long as wide.....*Cladosiphon filum*
28b. Outer cells 20 times as long as wide .....*Sauvageaugloia ikomae*
29a. Presence of an intercalary, sub-apical meristem 31
29b. Intercalary transverse divisions not restricted to a subapical meristem.....30
30a. Plurilocular sporangia, when present, formed by modification of the upper parts of assimilatory filaments .....*Myriogloia*
30b. Plurilocular sporangia pod-shaped, short-stiped, formed from the upper cells of a transition zone between the central axis and the assimilatory filaments .....*Levringia filiformis*
31a. Thallus with a very loose construction; gelatinous consistency 32

31b. Thallus with a firm construction; texture may be slippery but not gelatinous 34

32a. Thallus attached by means of a small disc; only unilocular sporangia present; rhizoidal filaments descending from inner cells at the base of the frond 33

32b. Thallus attached usually by means of a fairly well developed prostrate system; both unilocular and plurilocular sporangia present; rhizoidal filaments from inner cells of the frond base absent ..... *Heterosaundersella hattoriana*

33a. Thallus epiphytic on other algae ..... *Saundersella simplex*

33b. Thallus growing on rocks ..... *Saundersella saxicola*

34a. Thallus not exceeding 15 cm in length; occurrence of separate unilocular sporangiate and plurilocular sporangiate thalli 35

34b. Thallus exceeding 50 cm in length; occurrence only of unilocular sporangiate thalli 36

35a. Erect axes arising gregariously but not in tufts from a well developed prostrate system; erect axes flaccid and hollow; plurilocular sporangia terminated by usually two enlarged sterile cells. ..... *Analipus filiformis*

35b. Erect axes cespitose, arising in tufts from a rather small holdfast; erect axes are stiff, firm, with a limited central cavity; plurilocular sporangia terminated by a small sterile cell ..... *Myelophycus simplex*

36a. Thallus 1–2 mm broad, attached by a small disc; true hyaline hairs present; unilocular sporangia ovoid or pyriform growing on the surface cells of the thallus, from which assimilatory filaments also arise; cells of medulla not with thickened walls..... *Chordaria flagelliformis* f. *chordaeformis*

36b. Thallus to 5 mm broad, attached by a well developed confluent base; unilocular sporangia elongated or clavate, borne usually on a segment of the lower portion of the assimilatory filaments; medullary filaments with especially thickened walls..... *Pseudochorda nagaii*

TAXONOMIC ARRANGEMENT OF GENERA TREATED

Chordariales
- Chordariaceae
  - *Analipus filiformis*
  - *Chordaria flagelliformis* f. *chordaeformis*
  - *Cladosiphon filum*
  - *Heterosaundersella hattoriana*
  - *Levringia filiformis*
  - *Myelophycus simplex*
  - *Myriogloia intestinalis*
  - *M. lindaueri*
  - *M. simplex*
  - *Nemacystus subsimplex*

Pseudochorda nagaii
Saundersella saxicola
S. simplex
Sauvageaugloia ikomae
Suringaria harveyana
Sporochnales
Sporochnaceae
Bellotia simplex
Tomaculopsis herbertiana
Scytosiphonales
Scytosiphonaceae
Colpomenia sinuosa f. *deformans sensu* S. & G. (1924).
Scytosiphon crispus
S. dotyi
S. lomentaria
S. pygmaeus
Utriculidium durvillei
Dictyosiphonales
Striariaceae
Stictyosiphon subsimplex
Punctariaceae
Adenocystis utricularis
Asperococcoccus fistulosus
A. scaber
A. turneri
Corycus lanceolatus
Litosiphon filiformis
L. pusillus
Melanosiphon intestinalis
Protasperococcus myriotrichiiformis
Delamareaceae
Delamarea attenuata
Halosiphonaceae
Halosiphon altae
H. tomentosus
Dictyosiphonaceae
Coilodesme cystoserirae
Dictyosiphon ekmani
Laminariales
Chordaceae
Chorda filum
C. tomentosa

DESCRIPTIVE ACCOUNT

Adenocystis utricularis (Bory) Skottsberg

Syn.: *Asperococcus utricularis* Bory in D'Urville

Asperococcus lessonii Bory
Adenocystis lessonii Hooker & Harvey
Cf. Papenfuss, 1964, p. 18 for additional synonyms.

Descr.: Naylor, 1955, pl. 11; Lindauer, Chapman and Aiken, 1961, p. 258, Fig. 67 (1–6); Skottsberg, 1907, p. 39, Figs. 34 and 35; Kjellman, 1889b, p. 8, Figs. 9–11 (as *Adenocystis lessonii*).

Distr.: New Zealand, Australia (Womersley, 1967), Chile, Argentina (Asensi, 1966), Subantarctic and Antarctic (Papenfuss, 1964).

Naylor (1955) carried out culture studies on this species with New Zealand material. She observed that a direct development of new plants appeared to occur, with some accessory reproduction of the microscopic prostrate stages by plurilocular sporangia. These results indicated that this alga is not an alternate phase of *Utriculidium durvillei*, as had been suggested by Skottsberg (1907).

Analipus filiformis (Ruprecht) Papenfuss

Syn.: *Haplosiphon filiformis* Ruprecht
Chordaria filiformis Yendo
Heterochordaria filiformis (Yendo) Tokida
Analipus fusiformis Kjellman

Descr.: Kjellman, 1889a, p. 49, pl. 7, Figs. 6–12; Papenfuss, 1967, p. 320; Wynne, 1971, p. 169, Figs. 1–3, 5 & 6.

Distr.: northern rim of the Pacific Ocean (Bering Island, the Aleutians, the Pribilofs); Ochotsk Sea; northern Japan.

The erect axes of this species are developed from an extensive (20–30 cm in diameter) prostrate system, consisting of branching cylindrical haptera, which are closely coherent and constitute the perennating phase of this alga. This basal system is a distinctive feature for this genus and is easily recognized in field specimens. However, pressed herbarium specimens may lack the basal portion.

Asperococcus

Key to Cylindrical Species

1a. Thalli not exceeding 1 cm in length, remaining solid..... *A. scaber*
1b. Thalli usually exceeding 10 cm in length, becoming hollow 2
2a. Thalli usually less than 5 mm in diam., tubular, of firm consistency..... *A. fistulosus*
2b. Thalli 5–20 (or more) mm in diam., saccate, of delicate texture..... *A. turneri*

Asperococcus fistulosus (Hudson) Hooker

Syn.: *Ulva fistulosa* Hudson
Conferva echinata Mertens in Roth
Asperococcus echinatus (Mert. in Roth) C. Agardh
Encoelium echinatum (Mert. in Roth) Kützing
Encoelium fistulosum (Hudson) Kützing

Descr.: Harvey, 1849, pl. 194; Hamel, 1931–39, p. 222, Fig. 43VII; Rosen-

vinge and Lund, 1947, p. 43, Fig. 15; Kylin, 1947, p. 76, pl. 11, Fig. 37; Taylor, 1962, p. 169, pl. 15, Fig. 7, & pl. 16, Figs. 5 & 6 (these as *A. echinatus*); Reinke, 1889–92, p. 7, pl. 4 (as *A. echinatus* var. *filiformis*); Edelstein, Wynne and McLachlan, 1970, p. 7, Figs. 17 & 18; Kützing, 1859, p. 3, pl. 5, Figs. e-h (as *Encoelium echinatum*), and p. 3, pl. 6, Figs. c & d (as *Encoelium fistulosum*).

Exsicc.: Phyc. Bor.-Am. 128.

Distr.: temperate North Atlantic (New England, Canada, Scandinavia, France); North Sea; Baltic Sea

Parke and Dixon (1964) have regarded the various forms of this species (e.g., f. *vermicularis* Griffiths ex Harvey; f. *villosa* Kylin; var. *filiformis* Reinke) as insufficiently distinct to justify their recognition.

Asperococcus scaber Kuckuck

Descr.: Kuckuck, 1899a, p. 18, Figs. 1–4, pl. 8.

Distr.: Adriatic and Mediterranean Seas; United Kingdom.

This minute species attains only 1 cm in height and does not become hollow like the other species of the genus. Its myrionematoid basal disc is also distinctive. In transection four large medullary cells can be observed, and both plurilocular and unilocular sporangia may occur on the same thallus.

Asperococcus turneri (Dillwyn ex Smith) Hooker

Syn.: *Ulva turneri* Dillwyn ex Smith
Asperococcus bullosus Lamouroux
Encoelium bullosum (Lamouroux) C. Agardh

Descr.: Harvey, 1846, pl. 11; Thuret and Bornet, 1878, p. 16, pl. 6; Newton, 1931, p. 172, Fig. 107; Hamel, 1931–1939, p. 223; Kylin, 1947, p. 75, pl. 11, Fig. 38 (all as *A. bullosus* except Harvey).

Distr.: European North Atlantic (Norway, Sweden, Great Britain, the Netherlands, France, Spain); North Sea; Baltic Sea; Mediterranean Sea; Adriatic Sea.

Bellotia simplex Denizot

Descr.: Denizot, 1965, p. 67, pl. 2, Figs. 1–4.

Distr.: New Caledonia.

Chorda filum (Linn.) Stackh.

Syn.: *Fucus filum* Linn.
Scytosiphon filum (Linn.) C. Agardh

Descr.: Stackhouse, 1801, p. 40, pl. 10 (as *Fucus filum*); Harvey, 1846, pl. 107; Kützing, 1858, p. 6, pl. 14, Fig. a; Reinke, 1891, p. 35, pls. 26–28; Kylin, 1947, p. 79, pl. 14, Fig. 46; Taylor, 1962, p. 176, pl. 14, Fig. 3, & pl. 15, Fig. 1; Okamura, 1936, p. 243, Fig. 134; Tokida, 1954, p. 112.

Exsicc.: Phyc. Bor.-Amer. 831.
Distr.: common in cold-temperate waters of North Atlantic, North Pacific, Arctic Sea, and Bering Sea: Asia, North America, Europe. (Cf. Kjellman, 1883; Zinova, 1953; Druehl, 1970; South and Burrows, 1967).

Zinova (1953) recognized the following forms: f. *typica* Kjellm., f. *crassipes* Kjellm., f. *abbreviata* (Aresch.) Zin., and f. *subtomentosa* Aresch.

Chorda tomentosa Lyngbye

Syn.: *Chorda filum* f. *tomentosa* (Lyngbye) Areschoug
Descr.: Sundene, 1963, pls. 3 & 4; Taylor, 1962, p. 175; Reinke, 1891, p. 35, pl. 29; Harvey, 1846, pl. 107; Kützing, 1858, p. 7, pl. 14, Fig. b (the latter two as *C. filum* var. *tomentosa*).
Exsicc.: Phyc. Bor.-Am. 483.
Distr.: similar distribution pattern to that of *C. filum*.

Sundene (1963) observed that the gametophyte of *Chorda tomentosa* in culture is monoecious, thus differing from *C. filum*, which is dioecious (South and Burrows, 1967). The controversial relationship of this species to *Halosiphon tomentosus* is discussed under that species.

Chordaria flagelliformis (Mueller) C. Agardh f. **chordaeformis** Kjellman

Descr.: Kjellman, 1877, p. 28, pl. 1, Figs. 13–15; Tokida, 1934, p. 17, pl. 1; Inagaki, 1958, p. 154, Fig. 58; Kylin, 1940, Figs. 21A & B; Kylin, 1947, pl. 5, Fig. 19.
Distr.: Spitsbergen, Siberia, northern Japan, Kurils.

This form of the fairly cosmopolitan *Chordaria flagelliformis* may be simple or sparsely branched.

Coilodesme cystoseirae (Ruprecht) Setchell & Gardner

Syn.: *Asperococcus cystoseirae* Ruprecht
Encoelium cystoseirae (Ruprecht) Kützing
Coilodesme linearis Saunders
Descr.: Ruprecht, 1851, p. 370; Saunders, 1901, p. 421, pl. 48 (as *C. linearis*); Tokida, 1954, p. 109; Setchell & Gardner, 1925, p. 583; Yamada, 1938, p. 119, pl. 19.
Exsicc.: Phyc. Bor.-Am. 824 (as *C. linearis*); 1128.
Distr.: northwest Pacific (Hokkaido, Kurils, and Sakhalin) and the Ochotsk Sea; northeast Pacific (Alaska).

Colpomenia sinuosa f. **deformans** sensu Setchell & Gardner (1924)

Descr.: Setchell and Gardner, 1924, p. 726, pl. 19, Figs. 61 & 62; Wynne, 1972, Fig. 1.
Distr.: Gulf of California, Mexico.

Setchell and Gardner (1924) and Dawson (1966) have referred a distinctive form of *Colpomenia* occurring in the Gulf of California to *Colpomenia sinuosa* f.

deformans Setchell & Gardner. This alga consists of a cluster of 6–12 finger-like, inflated sacs arising from a well developed basal attachment. The sacs are delicate in texture and are tapered at the base. Wynne (1972) discussed the status of this alga and concluded that it is different from Setchell and Gardner's (1903, p. 242, pl. 18, Figs. 13–15) original concept of this form, which was based upon Saunders' (1898) *Scytosiphon bullosus*[2] from Pacific Grove, California. However, he refrained from describing this form as a new species pending further study.

Corycus lanceolatus (Kützing) Skottsberg

Syn.: *Phycolapathum lanceolatum* Kützing
Corycus nigrescens Kjellman
Corycus prolifer J. Agardh ex Kjellman
Descr.: Kjellman, 1889b, p. 18, Figs. 24–28 (as *Corycus nigrescens*); Skottsberg, 1907, p. 31, Figs. 28–32.
Distr.: Chile (Levring, 1960), Argentina (Asensi, 1966), Subantarctic and Antarctic (Papenfuss, 1964).

Cladosiphon filum (Harvey) Kylin

Syn.: *Mesogloia filum* Harvey
Bactrophora filum (Harvey) J. Agardh
Castagnea filum (Harvey) Kuckuck
Descr.: Agardh, J., 1881, p. 24, pl. I, Fig. 4 (as *Bactrophora filum*); Kuckuck, 1929, p. 50, Figs. 61 & 62 (as *Castagnea filum*).
Distr.: southern Australia, including Tasmania (Womersley, 1967).

Delamarea attenuata (Kjellman) Rosenvinge

Syn.: *Scytosiphon attenuatus* Kjellman
Physematoplea attenuata (Kjellman) Kjellman
Delamarea parodoxa Hariot
Descr.: Kjellman, 1883, p. 259, pl. 26, Figs. 1–5 (as *Scytosiphon attenautus*); Lund, 1959, p. 100, Figs. 18 & 19; Taylor, 1962, p. 168; Jaasund, 1965, p. 99, Fig. 32. Rosenvinge and Lund, 1947, p. 24, Figs. 7 & 8.
Distr.: circumboreal and subarctic; North Atlantic (Norway, Denmark, Spitsbergen, Greenland, Newfoundland); North Pacific (Alaska; cf. Johansen, 1971).

Zinova (1953) established a distinct family for this genus and later (1954) added to it three other genera, *Cladothele*, *Coelocladia*, and *Stschapovia*. Lund (1959) set up the Delamareales on the basis of its polystichous construction, presence of unilocular sporangia and numerous discoid chloroplasts per cell, and

[2] Currently recognized as *Colpomenia bullosus* (Saunders) Yamada, this species ranges in form from flattened caverous thalli to erect balloon-like sacs (cf. Setchell & Gardner, 1925, p. 542). The latter form would fall into the category of unchanched cylindrical brown algae. Wynne (1972) pointed out the means to distinguish this species from the above alga.

an alleged isomorphic life history (cf. Wynne, 1969, p. 49, for further comments).

Dictyosiphon ekmani Areschoug

Descr.: Collins, 1900, p. 162; Kylin, 1947, p. 79. pl. 14, Fig. 45; Taylor, 1962, p. 172; Jaasund, 1965, p. 96, Figs. 30 & 31.
Distr.: Scandinavia, Iceland (Munda, 1972), Arctic (Zinova, 1953), New England and eastern Canada (Taylor, 1962).
Exsicc.: Phyc. Bor.-Am. 533.

Jaasund (1965) expressed doubt that this species represents a true *Dictyosiphon* since no parenchymatous tissue like that of *D. foeniculaceus* is produced.

In addition to this simple to subsimple species of *Dictyosiphon*, Taylor (1962) referred to *D. chordaria* Aresch. as being simple to sparingly branched. Most other authors (e.g., Zinova, 1953; Kylin, 1947) refer to only branched specimens of this latter species.

DeToni (1895) listed *Dictyosiphon filiformis* Foslie as a simple species from northern Norway. Dr. E. Jaasund of Tromsö has informed me that he examined all three sheets of Foslie's *Dictyosiphon* (*Coilonema*) *filiformis*, now located in the museum in Trondheim and found that the specimens are "clearly *Scytosiphon*, a poorly developed form that grows in rock pools in the upper part of the intertidal zone."

Halosiphon altae Jaasund

Descr.: Jaasund, 1957, p. 213, Fig. 5; 1965, p. 104.
Distr: northern Norway.

Halosiphon tomentosus Jaasund

Descr.: Jaasund, 1957, p. 212, Figs. 1, 3, & 4b-d; 1965, p. 103, Fig. 33.
Distr.: northern Norway; Murman coast of Siberia (Perestenko, 1963).

This taxon was originally based upon *Chorda tomentosa* Lyngbye, but later the author (Jaasund, 1965) regarded it as an independent taxon, retaining the specific epithet. The validity of this genus has been doubted by Sundene (1963), but Perestenko (1963) has supported the existence of a separate entity.

In addition to the differences listed in the Key, Jaasund (1957) also figured for *Halosiphon* a life history including a microscopic generation bearing plurilocular gametangia.

Heterosaundersella hattoriana Tokida

Descr.: Tokida, 1942, p. 84, Figs. 2a-f & 3; 1954, p. 95, pl. 13, Fig. D.
Distr.: northwestern Pacific (endemic to Sakhalin).

This alga is closely related to *Saundersella simplex* but differs in several anatomical respects: a dimorphic construction, including a prostrate portion over the surface of the host; the absence of descending rhizoidal filaments from the inner

cells at the base of the frond; and the occurrence of both plurilocular and unilocular sporangia.

Levringia filiformis Kylin

Descr.: Kylin, 1940, p. 15, pl. 1, Fig. 3.
Distr.: South Africa.

Litosiphon filiformis (Reinke) Batters

Syn.: *Pogotrichum filiforme* Reinke
Descr.: Reinke, 1892, p. 62, pl. 41 (as *Pogotrichum filiforme*); Hamel, 1931–1939, p. 219, Figs. 43VIII-X;Kylin, 1947, Fig. 60B-D.
Exsicc.: Phyc. Bor.-Am. 1035.
Distr.: Widely distributed on both sides of North Atlantic.

Litosiphon pusillus (Carm. ex Hook.) Harvey

Syn.: *Asperococcus pusillus* Carm. ex Hooker
Punctaria pusillus (Carm. ex Hook.) Crouan & Crouan
Chlorosiphon pusillus (Carm. ex Hook.) Harvey
Descr.: Harvey, 1851, pl. 270; Newton, 1931, p. 180.
Hamel, 1931–39, p. 217, Fig. 43IV-VI; Rosenvinge and Lund, 1947, p. 15, Fig. 3; Kylin, 1947, p. 74, Fig. 60A, pl. 10, Fig. 33.
Distr.: Sweden, Denmark, France, United Kingdom.

Melanosiphon intestinalis (Saunders) Wynne

Syn.: *Myelophycus intestinalis* Saunders
Descr.: Saunders, 1901, p. 420, pl. 47 (as *Myelophycus intestinalis*); Wynne, 1969, p. 45, Figs. 11 & 12, and pl. 24; Edelstein, Wynne, and McLachlan, 1970, Figs. 1–16.
Exsicc.: Phyc. Bor.-Am. 872 and 1129.
Distr.: northwestern Pacific (Kamchatka, Okhotsk Sea, Hokkaido, Sakhalin); northeastern Pacific (Alaska to central California); northwestern Atlantic (Nova Scotia, Massachusetts).

Myelophycus simplex (Harvey) Papenfuss

Syn.: *Chordaria simplex* Harvey
Myelophycus caespitosus Kjellman
Descr.: Kjellman, 1893, p. 202, Fig. 141 (as *Myelophycus caespitosus*); Papenfuss, 1967, p. 323, Fig. 1; Wynne, 1969, p. 43, pls. 22 & 23; Chihara, 1970, p. 31, pl. 16, Fig. 1.
Distr.: Japan

Myriogloia

Key to Simple (or Sparingly Branched) Species

1a. Thalli 30–75 cm long; unilocular sporangia more than 130 μ long..... *M. lindaueri*

1b. Thalli less than 30 cm long; unilocular sporangia less than 120 μ long.... 2

2a. Thallus up to 30 cm long, 1–2 mm thick; assimilatory filaments to to 1 mm long; unilocular and plurilocular sporangia on same plant ..... *M. intestinalis*

2b. Thallus 8–15 cm long, 5–13 mm thick; assimilatory filaments 1–2 mm long; plurilocular sporangia unknown ..... *M. simplex*

Myriogloia intestinalis Harvey) Lindauer, Chapman & Aiken

Syn.: *Mesogloia intestinalis* Harvey
Myriocladia chorda J. Agardh
Myriogloia chorda (J. Agardh) Kuckuck

Descr.: Lindauer, Chapman, and Aiken, 1961, p. 224, Fig. 47; Levring, 1939, Figs. 2, 3 D & E (as *Myriogloia chorda*).

Distr.: New Zealand.

Myriogloia lindaueri Kylin

Descr.: Kylin, 1940, p. 12, Fig. 8B-D; Lindauer, Chapman, and Aiken, 1961, p. 225, Figs. 48 & 49.

Distr.: New Zealand.

Myriogloia simplex (Segawa & Ohta) Inagaki

Syn.: *Tinocladia simplex* Segawa & Ohta

Descr.: Inagaki, 1958, p. 125, Figs. 31–34.

Distr.: Japan.

Nemacystus subsimplex Kylin

Descr.: Kylin, 1940, p. 48, Figs. 26 A & B, pl. 8, Fig. 19.

Distr.: South Africa.

As the specific epithet indicates, this species may vary between unbranched and sparingly branched conditions. In a given population both types of individuals may be encountered.

Protasperococcus myriotrichiiformis Sauv.

Syn.: *Myriotrichia Protasperococcus* Berthold ex Kuckuck

Descr.: Kuckuck, 1899b, p. 36, Figs. 10 & 11, pls. 10 & 11 (as *Myriotrichia Protasperococcus*); Sauvageau, 1931, p. 81, Figs. 13–15; Hamel, 1931–39, p. 233, Fig. 46, I & VII.

Distr.: Adriatic and Mediterranean Seas.

Pseudochorda nagaii (Tokida) Inagaki

Syn.: *Chordaria nagaii* Tokida
Descr.: Tokida, 1938, p. 213, Figs. 1–4; Nagai, 1940, p. 47 (both as *Chordaria nagaii*); Inagaki, 1958, p. 175, Figs. 74–76.
Distr.: northwestern Pacific (Sakhalin, Kurils).

This alga superficially resembles *Chorda filum*, but its internal anatomy is quite different from the kelp genus in that it is pseudoparanchymatous with multicellular assimilatory filaments. It differs from *Chordaria* in lacking true hairs and in the position of the unilocular sporangia.

Saundersella saxicola (Okamura & Yamada) Inagaki

Syn.: *Gobia saxicola* Okamura & Yamada
Descr.: Okamura, 1937, p. 79, pl. 345, Figs. 4 & 5 (as *Gobia saxicola*); Inagaki, 1958, p. 161, Fig. 64.
Distr.: Japan.

Saundersella simplex (Saunders) Kylin

Syn.: *Mesogloia simplex* Saunders
Gobia simplex (Saunders) Setchell & Gardner
Descr. Saunders, 1901, p. 423, pl. 50, Figs. 2–4 (as *Mesogloia simplex*); Setchell and Gardner, 1925, p. 576, pl. 42, Fig. 58, and pl. 78B (as *Gobia simplex*); Tokida, 1942, Fig. 2g; Inagaki, 1954, p. 159, Figs. 61–63 and pl. IX. Fig. 2.
Distr.: Japan; Alaska to Washington.

Sauvageaugloia ikomae (Narita) Inagaki

Syn.: *Castagnea ikomae* Narita
Descr.: Narita, 1936, p. 386, Figs. 1 & 2 (as *Castagnea ikomae*); Inagaki, 1954, p. 13, Fig. 10; 1958, p. 142, Fig. 48.
Distr.: Japan

Scytosiphon

Key to the Species

1a. Thalli usually constricted (except f. *complanatus*), to 50 cm long; colorless unicellular paraphyses present ..... *S. lomentaria*
1b. Thalli rarely or inconspicuously constricted, never exceeding 12 cm; colorless unicellular paraphyses absent 2
2a. Thalli to 12 cm long, flaccid ..... *S. dotyi*
2b. Thalli to 1 cm long 3
3a. Thalli 4–7 mm long, not noticeably torsioned; central cavity narrow or non-existent; tufts of true hairs present; sporangia up to 15 compartments long ..... *S. pygmaeus*

3b. Thalli to 1 cm long, conspicuously torsioned and crisp in texture; hollow central portion; true hairs absent; sporangia 3–6 compartments long..... .....*S. crispus*

Scytosiphon crispus Skottsberg

Descr.: Skottsberg, 1907, p. 35, Fig. 33.
Distr.: Falkland Islands.

Scytosiphon dotyi Wynne

Syn.: Cf. Wynne (1969).
Descr.: Wynne, 1969, p. 34, pl. 18 a-d.
Distr.: west coast of North America (Oregon to Baja, California).

Scytosiphon lomentaria (Lyngbye) J. Agardh

Syn.: *Chorda lomentaria* Lyngbye
Descr.: Setchell & Gardner, 1925, p. 531, pl. 44, Figs. 72 & 74; Smith, 1944, p. 129, pl. 19, Figs. 1 & 2; Taylor, 1962, p. 168, pl. 15, Fig. 2, pl. 16, Fig. 3; Wynne, 1969, pls. 14–17. Harvey, 1851, pl. 285 (as *Chorda lomentaria*); Kützing, 1858, p. 7, pl. 14, Fig. C (as *Chorda filum* var. *lomentaria*; var. *lomentacea* in text).
Exsicc.: Phyc. Bor.-Am. 323, 1235, 1389, and 2079.
Distr.: cosmopolitan in northern and southern hemispheres; cold and temperate seas, except for tropics.

The typical form of this species is characteristically constricted at regular intervals and has colorless paraphyses scattered among the plurilocular sporangia; forma *complanatus* Rosenvinge has the paraphyses but lacks the constrictions. A crustose stage bearing unilocular sporangia has been demonstrated to be an alternate phase in the life history of this species (Nakamura, 1965; Tatewaki, 1966; Wynne, 1969), although there is disagreement as to its relationship to the large tubular thallus.

Scytosiphon pygmaeus Reinke

Descr.: Reinke, 1889, p. 17, pl. 14; Jaasund, 1964, p. 129, Fig. 1
Distr.: Baltic Sea; Norway.

Loiseaux (1970) observed that a small *Scytosiphon* similar to *S. pygmaeus* developed in cultures obtained from unilocular sporangia of a California *Streblonema*. However, *S. pygmaeus* has not yet been collected in nature in the Pacific.

Stictyosiphon subsimplex Holden

Descr.: Holden, 1899, p. 198, pl. 9, Figs. 1–6; Taylor, 1962, p. 158; Edwards, 1971, p. 27, Figs. 84–86.
Exsicc.: Phyc. Bor.-Am. 630
Distr.: eastern coast of North America (Nova Scotia and Quebec) to southern Florida; Gulf of Mexico (Texas; Tamaulipas, Mexico).

Initially, circumstantial evidence but more recently culturing studies (pers. observ.) have implicated *Stictyosiphon subsimplex* in the life history of *Farlowiella onusta* (= *Myriotrichia subcorymbosa*) of the Ectocarpaceae. This fact would suggest that *S. subsimplex* does not fit with *Stictyosiphon*. The oldest epithet applicable to this taxon would be Kützing's *Ectocarpus onustus* (1849, p. 457), which was described on the basis of a collection by Lenormand from Galveston, Texas.

Suringaria harveyana (J. Agardh) Kylin

Syn.: *Liebmannia harveyana* J. Agardh
L. australis var. *simpliuscula* Harvey in Hooker
Descr.: J. Agardh, 1881, p. 52, pl. 2, Fig. 4 (as *Liebmannia harveyana*); Kylin, 1940, p. 36, plg. 6, Fig. 14.
Distr.: southern Australia (Womersley, 1967).

Tomaculopsis herbertiana Cribb

Descr.: Cribb, 1960, p. 18, pl. 7, Figs. 1–8.
Distr.: Queensland, Australia.

Cribb (1960) distinguished this genus from the seven other genera of *Sporochnales* in having the axis unbranched. Denizot (1965) later described an unbranched *Bellotia* (*B. simplex*; see above) from New Caledonia but did not refer to Cribb's genus. The two species appear to be different in that *B. simplex* is uniformly cylindrical and attains 6 cm in height, whereas *T. herbertiana* has an enlarged distal end and is only 1.5 cm tall. (It is to be noted that the description was based upon a single specimen.) Both species have simple fertile filaments. The basis upon which *Tomaculopsis* was erected needs re-evaluation.

Utriculidium durvillei (Bory) Skottsberg

Syn.: *Asperococcus D'Urvillaei* Bory
Adenocystis D'Urvillaei Hooker & Harvey
Scytosiphon Urviellei Trévisan
Encoelium Durvillaei (Bory) Kützing
Descr.: Skottsberg, 1907, p. 36, Figs. 34 & 35; 1921, p. 42, Figs. 16 g-i; Lindauer, Chapman and Aiken, 1961, p. 259, Fig. 67(7–9); Kützing, 1859, p. 3, pl. 6, Fig. e (as *Encoelium Durvillaei*).
Distr.: various islands in the sub-Antarctic (Papenfuss, 1964).

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A GRADIENT APPARATUS FOR THE STUDY OF SALINITY PREFERENCE OF SMALL BENTHIC AND FREE SWIMMING ORGANISMS

Richard K. Keiser, Jr. and David V. Aldrich

Texas A&M Marine Laboratory, Galveston, Texas 77550

ABSTRACT

An experimental salinity gradient system has been developed to meet a need in efforts to determine the salinity preference of small benthic and estuarine organisms. In the described apparatus a slanting tank provides a homogeneous bottom for benthic organisms throughout the full range of test salinity levels. Continuous gradients produced in this apparatus are shown to be quite stable for several days. They also differ from earlier systems in lacking either physical barriers, salinity discontinuities, or water currents. The apparatus can also be used to determine salinity preferences of small free-swimming organisms.

INTRODUCTION

It is generally accepted that salinity is a significant ecological factor, directly or indirectly determining the distribution of many species. In view of this, a surprising dearth of experimentally derived information exists regarding the salinity preference of aquatic animals. The scarcity of such research results from the complexity or unsuitability of existing experimental apparatus.

Our interest in determining the salinity preference of postlarval penaeid shrimp (*Penaeus aztecus*) led us to examine existing methods. Finding these inappropriate for the organism we wished to study, we developed a more suitable apparatus. It not only meets our needs, but is also applicable to the study of a variety of other organisms whose salinity preferences have not been previously examined.

PREVIOUSLY DESCRIBED APPARATUS

Two general types of salinity choice apparatus are referred to in the literature. The first type includes multiple chamber (or level) setups in which chambers (or levels) are separated by sharp discontinuities. Choice experiments of the first type were used to test the salinity preference of oligochaetes (Jansson 1962), fish (Baggerman 1957, 1960, 1963; Houston 1957; McInersey 1964) and amphipods (McLusky 1970; Lagerspetz and Mattila 1961). The halves of a 2-chambered container were filled with waters of differing salinity. Animals were introduced into one side and were free to move between the containers via a shallow layer of water at the surface. Hill and Holland (1971) modified the apparatus of Hodgson (1951) and Jones (1947) for testing salinity preference. Fish were placed in a horizontal cylinder, and waters of different salinities were introduced

at each end. The two solutions maintained a sharp interface at the middle of the chamber; however there were no barriers to obstruct the movement of the fish. Creutzberg (1961) offered eels the opportunity to choose between four different solutions. The elvers were placed in a chamber receiving inflow from four bottles. A preference for a particular solution was demonstrated by the elvers' swimming up-current towards the source of that solution.

Other researchers tested the salinity response of various organisms to discontinuity layers in vertical cylinders. The salinity discontinuity layers were created by layering the solutions one on top of the other, placing the more saline at the bottom. Animals were introduced into the cylinder and were free to move through the discontinuity layers. This apparatus has been used to test the salinity preference of lobster larvae (Scarratt and Raine 1967), postlarval pink shrimp (Hughes 1969), and a variety of zooplankton (Harder 1968; Lance 1962). Hurley and Woodall (1968) used a 425-gallon vertical tank containing six discontinuity layers to test the salinity preference of young pink salmon. Staaland (1969) tested the salinity preference of whelks in a horizontal tank. Salinity discontinuities were maintained by a series of baffles that divided the tank into eight interconnecting compartments.

The second type of salinity preference equipment includes continuous gradients which lack discontinuities. Such continuous gradients have proven quite valuable in experimental studies of temperature preference (Doudoroff 1938; Norris 1963). A useful characteristic of smooth gradients is the absence of discrete physical barriers such as baffles or other sharp discontinuities in the experimental chamber. This feature permits ready availability to experimental organisms of *all* levels of the selected gradient range. Experimental ranges may include and extend beyond levels associated with the organism's natural distribution.

Despite the potential utility of such salinity gradients, they have been rarely used. We have, in fact, found only two references to preference work conducted in continuous horizontal gradients of salinity. Doudoroff (1938) tested fish in a dynamic gradient established by continuously adding water of different salinity at 14 points in a rectangular aquarium. Hansen (1972) using a fluvarium (Hoglund 1951) differentially mixed salt and fresh water to produce a horizontal gradient of salinity.

Existing horizontal gradients were unsatisfactory for testing the salinity preference of postlarval *Penaeus aztecus*. Small forms such as larval crustaceans and fishes are relatively weak swimmers and cannot control their position within a gradient employing currents. Gentler currents would also present a problem, for rheotactic responses of most of these organisms have not been clearly defined.

Aldrich (1963) established a continuous salinity gradient ranging from 1‰ to 70‰ in a cylindrical 7–l, 1.2 m vertical column to study postlarval penaeid shrimp. This arrangement was not completely satisfactory because the crustacean larvae, having a higher specific gravity than seawater, tended to sink in the vertical column. This tendency required them to swim continuously to maintain their position in the column (abnormal behavior). From this earlier work evolved the apparatus described below.

NEW APPARATUS

Description

The above problem encountered with Aldrich's (1963) vertical column was eliminated by making a resting place or "bottom" available to shrimp in the gradient. This was accomplished simply by slanting the gradient tank at an angle of 25° (Fig. 1). The sloping tank permits postlarval shrimp to rest at any level in the gradient, using as a "bottom" what was a vertical wall when the tank was upright. Another problem, the presence of "blind spots" in the cylindrical chambers, was eliminated through the use of square cross-sectional design.

The experimental tanks were constructed of 0.6 cm Plexiglas with inside dimensions 3.6 m x 10.2 cm wide x 10.2 cm high, open at one end. The 3.6 m long sides were made by joining two pieces of Plexiglas and overlapping the joints with 4-cm wide Plexiglas braces. The location of the joints was varied between adjoining walls to further strengthen the tank (Fig. 2.A.(1)). The aquaria rested on wooden boards 1.8 x 22.8 cm ("1 x 10" in) and were stacked one on top of the other on a framework of 3.7 x 14.0 cm ("2 x 6" in) boards. All wooden supports were painted dull black to reduce light reflection. Six 122 cm (4 ft) 40-watt Rapid Start fluorescent fixtures were mounted on a 1.8 x 28.4 cm ("1 x 12" in) board in 2–3.6 m rows and positioned 43.3 cm behind the tanks. The distance between

FIG. 1. Front view of assembled salinity gradient apparatus showing tanks, supports and lights.

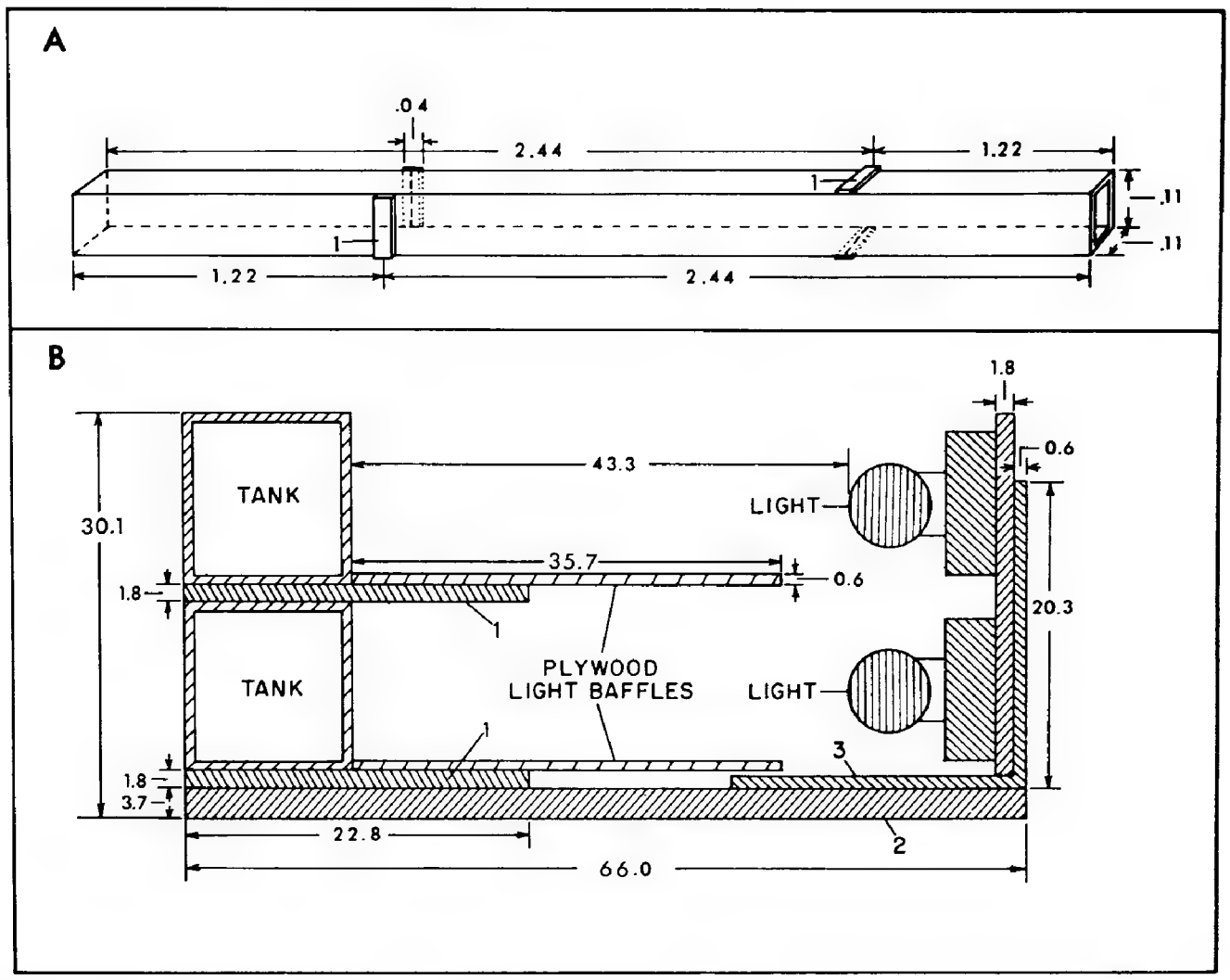

FIG. 2. A. Diagram showing detail of tank. (1) external Plexiglas brace at joints. All dimensions in meters. B. Detailed cross-section of apparatus. (1) longitudinal supports, (2) transverse support, (3) angle iron brace. All dimensions in centimeters.

the back surface of each tank and the lights was spanned by 0.6 cm plywood which directed the illumination (Fig. 2.B). A 7.6 cm space between the board and the lamps allowed for dissipation of the heat generated by the bulbs. Initially, the apparatus had a plywood cover; however, experimentation showed that a lid was unnecessary in a darkened room. Lines parallel to the floor were affixed to the outside of the tanks at 5 cm intervals. This provided a grid with which to define the position of the animals in the tank. One reason for constructing tanks of these dimensions was to maximize the use of available space. The overall dimensions of the apparatus—3.4 m long x 1.8 m high x 0.7 m wide—just allow for its placement in an average sized temperature control room. These tanks were also about the maximum size that could be conveniently moved by two persons for positioning and cleaning.

Forty-watt red fluorescent lamps provided the only illumination during our experiments. Waterman (1961) noted that the few marine crustaceans which have been examined possessed photopigments that would reduce their visual sensitivity to light of long wave lengths. This suggested that the use of red light might likewise minimize the sensitivity to visual stimuli of the penaeid shrimp we wished to study. The intensity of visual light emitted by fluorescent tubes decreases towards the ends and often differs among tubes. We used a photometer (model 250P; Science and Mechanics) to select six tubes of equivalent intensity.

The voltage to the six tubes was regulated by a voltage controller (model 2603; Cole-Parmer Instrument Co.). With our particular model, a setting of 35 v gave satisfactory illumination. As the light intensity decreased through usage, the voltage was increased to maintain the initial level of illumination.

Gradient Preparation

Three stock solutions were used in each experiment. Two of these—the most saline water to be tested and water of the salinity to which the experimental animals had been acclimated—were prepared using distilled water and Instant Ocean (Aquarium Systems). The third stock solution was distilled water. All were aerated for at least 24 hours before using to assure oxygen saturation. The most saline stock solution (70‰ in our work) and the distilled water were used to provide the extremes in the gradient tank and all mixtures in between. The control tank was filled with the stock solution which would present no change in salinity to the experimental organisms. This tank was used to test the response of the animals to water pressure or other possible cues associated with the experimental apparatus. The experimental tank was identical to the control tank, except that it contained a salinity gradient ranging from the bottom to the top (70‰ to 0‰ in our case). The gradient tank was first filled to the 40 cm line with 70‰ solution. The remaining solutions—63, 56, 49, 42, 35, 28, 21, 14, 7, 0‰—were siphoned in that order into the tank using 4 mm i.d. plastic aquarium tubing. Each solution occupied a 10 cm region of the tank. As less dense solutions were added, the flow rate was adjusted using a pinch clamp to confine mixing to the top 5 cm of the preceding compartment. The mixing process was clearly visible with the back-lighted illumination of the apparatus. When filled to a level of 140 cm, the tanks held 38 l (10 gal). Filling of the gradient and control tanks required approximately 6 hours.

To eliminate possible discontinuities, a 3.6 m section of 1.3 cm i.d. PVC pipe, fitted at one end with a #13 rubber stopper, was slowly pushed down the water column to the 40 cm line. As the plunger passed through the water column, any deviations from the desired relationship between salinity and depth were minimized. A series of 15 cm to 30 cm long thrusts were sometimes required to smooth over a discontinuity.

Gradient Measurement and Adjustment

The gradient was measured using a 3.6 m long siphon fashioned of 30 cm pieces of 3 mm i.d. rigid plastic or glass tubing joined by short sections of flexible aquarium air tubing. The glass tubing was used at the lower end to provide weight, which facilitated introducing the siphon into the tank. Measurement was a two-person operation. One monitored the position of the siphon, measured the salinity of sample withdrawn, and recorded the data. The second person positioned the siphon in the tank and withdrew water samples. Salinity was measured at 10 cm intervals beginning at 20 cm from the tank bottom. When each desired level was reached, a 70 ml sample was drawn through the siphon to flush out water from the previous depth (Fig. 3). (The volume of the siphon was approxi-

FIG. 3. Measurement of the salinity gradient. The graduated cylinder contains siphon flushings. A sample is being dispensed from siphon in tank to refractometer for salinity determination. See text.

mately 60 ml.) The salinity of the new depth was measured using a Goldberg refractometer (American Optical Co.). The volume of water withdrawn during measurement (840 ml) was replaced by slowly siphoning in an equal volume of distilled water. After the tank was refilled to the 140 cm level, a surface sample

was taken with an eye dropper. At the termination of the experiment, this procedure was repeated, beginning at 140 cm and ending at 20 cm.

During measurement of the gradient, a graph was made of salinity vs depth. This relationship is usually quite linear. If salinity discontinuities do cause the slope of this line to deviate from linearity, the gradient can be adjusted by remixing the levels in question. The gradient was then remeasured beginning 10 cm below the adjusted region.

Introduction of Animals

A releasing device was designed to avoid exposing the animals to great salinity changes while introducing them into the tanks. It consisted of an outside cylinder (5.0 cm i.d. x 11.2 cm long) connected by a rubber stopper to Plexiglas tubing 1.6 m long and with 9 mm i.d. A Plexiglas rod 1.8 m long and 6 mm in diameter passed through the rigid tubing. To this rod were glued, 7 cm apart, a rubber stopper and a polyethylene-Plexiglas disc. Together they formed the releasing chamber (Fig. 4). Pushing on the rod while holding the sleeve tubing opened the chamber; pulling the rod closed it. To load the releaser with animals it was inverted and opened approximately 2.5 cm. The experimental organisms in about 75 cc of holding tank water were poured into the releaser. The chamber was filled, closed, and was lowered slowly, to avoid disturbing the gradient, into the tank to a depth corresponding to the salinity of the holding tank water. This

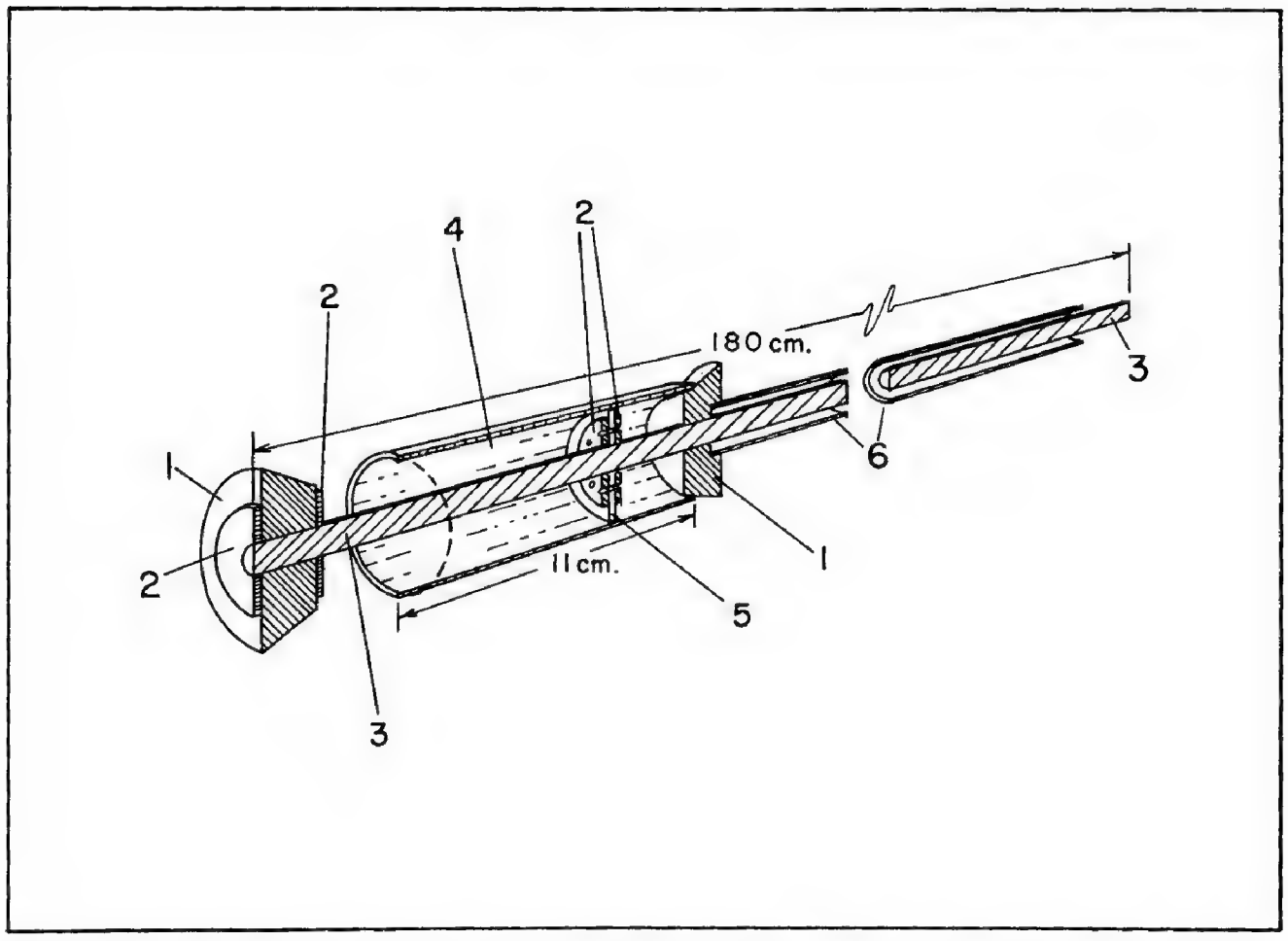

FIG. 4. Releasing device used to introduce animals into tanks. (1) no. 10 rubber stopper, (2) Plexiglas disc 4.0 × 0.6 cm, (3) Plexiglas rod 180 × 0.6 cm, (4) Plexiglas chamber 11.0 × 4.7 i.d., (5) polyethylene disc 4.7 × 0.3 cm, (6) Plexiglas tube 160 × 0.9 cm i.d.

depth was easily calculated from the graph of salinity vs depth. When the desired depth was reached, the chamber was opened, and the inside disc moved forward pushing the animals out. The releaser was closed and removed from the tank, withdrawing water of the same salinity and volume as was introduced with the animals. This procedure did not disturb the salinity gradient. Animals were similarly released in the control tank at the same depth as in the gradient tank.

Duration of the Experiment

During an experiment the tanks were not aerated nor was food provided. These two factors limit the duration of experiments. The size and number of animals that may be tested in the apparatus should also be considered. When 50 postlarval shrimp (8 to 16 mm) were used, the salinity gradient was stable for 3 days (Fig. 5). However, the gradient was significantly altered after 3 days by 50 larger postlarvae (13 to 25 mm). This does not preclude the use of this apparatus for testing salinity preference of such animals in fewer numbers or for shorter periods. We believe that 24 hours is sufficiently long to elicit most circadian or tidal rhythms that might affect distribution of animals within the tanks.

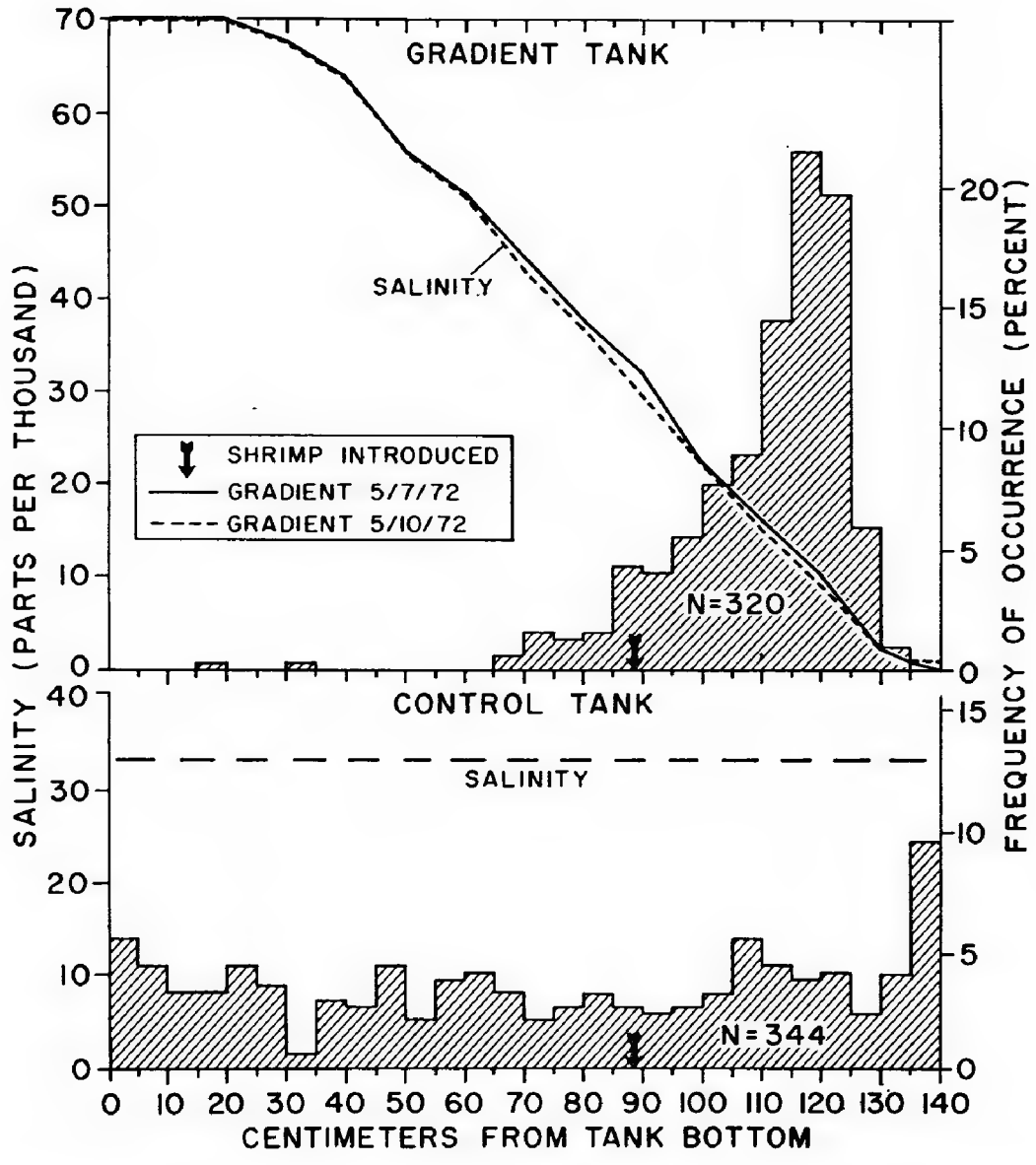

FIG. 5. Distribution of postlarval brown shrimp during a salinity preference experiment. Histograms represent seven observations of 46 animals in the gradient tank and 50 in the control tank. (Slight differences between theoretical and observed totals are due to the transparency of these shrimp and the low light levels used, which contributed to occasional counting errors.)

Typical Results

For one of our typical experiments we held a group of postlarval brown shrimp (*Penaeus aztecus*) for 3 days in the laboratory at 33‰. Then approximately 50 shrimp were placed in each of the apparatus tanks.

Beginning 2 hours after introduction, the postlarvae were observed for 1-hr periods spaced 6 hours apart. During each hour of observation, the number of shrimp in each 5 cm region of the tanks was recorded every 10 minutes. Figure 5 shows the frequency distribution for brown shrimp postlarvae in the gradient and control tanks for a 1-hr period. The solid and dotted lines in the figure indicate the stability of the salinity gradient during this 3-day experiment. The maximum difference between initial and final readings at any level was 2‰, but in general final levels were within 1‰ of initial readings.

The arrow indicates the point of release in both gradient and control tanks. This position corresponds to a salinity of 33‰. In the control tank, the animals were approximately uniformly distributed, whereas in the gradient tank, the shrimp showed a marked preference for a particular range of salinity. Our complete findings on the response of postlarval white and brown shrimp to continuous salinity gradients will form the basis of separate reports.

Our investigations have dealt largely with postlarval shrimp; however, discrete salinity preference or avoidance patterns have also been noted for three other estuarine animals—a fish, a mysid and a gastropod. We conclude that the described device can be used to determine the distribution patterns of many small, free-swimming or benthic organisms in continuous salinity gradients.

ACKNOWLEDGMENTS

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THE RELATIONSHIP BETWEEN THE PITUITARY CONTENT OF PROLACTIN AND BLOOD SODIUM LEVELS IN MULLET (*MUGIL CEPHALUS*) TRANSFERRED FROM SEA WATER TO FRESH WATER

Martin Sage

University of Texas Marine Science Institute, Port Aransas, Texas 78373

and

University of California Bodega Marine Laboratory, Bodega Bay, California 94923

ABSTRACT

Blood sodium levels in *Mugil* adapting to a transfer from sea water to fresh water stabilized within 24 hours. There was no change in the mean prolactin concentration of the pituitaries at any time from 30 min to 6 weeks following transfer of fish from sea water to fresh water. There were, however, significant changes in the correlation of pituitary prolactin content with blood sodium and body weight. Seawater fish have a pituitary prolactin content which shows no correlation with either body weight or blood sodium, whereas, in fish adapting to fresh water there is a negative correlation between prolactin and blood sodium as well as with body weight. In fish adapted to fresh water for one day or more there was a negative correlation of prolactin with blood sodium but no relationship to body weight. It is thus concluded that prolactin is involved both in the initial stages and the long term adaptation of *Mugil* to fresh water.

INTRODUCTION

Prolactin is necessary in many euryhaline teleosts for the survival in fresh water following hypophysectomy (see reviews by Ball, 1969; Sage and Bern, 1971). The mullet, *Mugil cephalus*, is a remarkably euryhaline fish being found in fresh, sea and hypersaline waters (Thomson, 1966; Blanc-Livni and Abraham, 1970; Abraham, 1971) and can be transferred rapidly between different salinities. Differences in the prolactin cells of the pituitaries of *M. cephalus* taken from different salinities are known (Leray, 1968; Blanc-Livni and Abraham, 1970; Abraham, 1971) and decreases in the prolactin content of pituitaries from mullet caught in increasing salinities have also been described (Blanc-Livni and Abraham, 1970).

The present investigation of the prolactin content of mullet pituitaries from fish adapting to fresh water was undertaken to determine whether there are changes in the pituitary prolactin content associated with the initial stages of adaptation to fresh water or whether changes in prolactin are a later consequence of such adaptations.

MATERIALS AND METHODS

Mugil cephalus were collected by cast net during their winter migration from the bays to the open seas of the Gulf of Mexico as they passed Port Aransas, Texas. Animals (ranging in weight from 136 to 178 g) were kept for 4 weeks in a concrete holding tank containing 100 m^3 of sea water and then abruptly transferred to 6m^3 fiberglass tanks of fresh water in groups of 4 to 6. Prolactin content of acetone dried pituitaries was determined by an assay (Sage & Bern, 1970, 1972) which depends on the dispersal of pigment in the xanthophores of *Gillichthys mirabilis* (Sage, 1970). These assays were carried out at the University of California, Bodega Marine Laboratory. Blood sodium, potassium and calcium were determined by flame photometry.

RESULTS

The results of blood ion analyses and pituitary prolactin contents are given in Table 1. Blood sodium fell initially on transfer of fish to fresh water, but by 24 hours it had risen slightly and stabilized at a level not significantly different to that seen in fish that had been kept for six weeks in fresh water. Pituitary prolactin contents showed no discernable trend with the time that fish had spent in fresh water.

Since prolactin may act by reducing surface permeability (see review by Ball, 1969) its release might be expected to show some correlation with body size and with blood sodium levels. It seemed possible that sudden changes in release of prolactin such as may result from an abrupt transfer of fish to fresh water may alter the amount of hormone in the pituitary. The possibility of a correlation was therefore investigated between the pituitary prolactin content and blood sodium levels and between prolactin and body weight.

For the purpose of these calculations of correlation coefficients the data were grouped into 3 categories.

1. Sea water fish.
2. Fish adapted to fresh water for 24 hours or more.
3. Fish in the initial stages of adapting to fresh water and which had been in fresh water for 30 mins to 4½ hours.

The correlation coefficients (Table 2) indicated a significant relationship between prolactin and body weight, and between prolactin and blood sodium in

TABLE 1

Blood ions (Meq/l.) and pituitary prolactin content of *Mugil cephalus* in sea water and at various times after transfer to fresh water. Results are means ± standard errors. Ions are expressed as mEq/l. and prolactin as log *Gillichthys* units/μg dry weight of pituitary

Time in fresh water	Na^+	K^+	Ca^{++}	Prolactin	n
(Zero = sea water)	159.3 ± 5.5	5.8 ± 0.36	1.73 ± 0.13	7.5 ± 0.8	12
30 min	155.3 ± 9.2	.....	.....	9.1 ± 1.7	4
1½ hr	149.8 ± 17.1	.....	.....	7.4 ± 2.0	4
3 hr	147.8 ± 2.5	4.99 ± 0.48	1.63 ± 0.24	.....	8
4½ hr	133.8 ± 15.0	.....	.....	8.8 ± 1.8	4
1 day	152.2 ± 5.7	.....	.....	4.4 ± 1.2	5
4 days	153.0 ± 4.3	.....	.....	8.6 ± 1.7	4
6 weeks	150.7 ± 1.8	5.07 ± 0.44	1.42 ± 0.07	6.8 ± 0.9	6

TABLE 2

Correlation coefficients (r) between pituitary prolactin content and body weight and blood sodium in *Mugil cephalus*

Correlation between	r	Significance
A. Animals adapted to sea water n = 12		
Prolactin and body weight	—0.24	n.s.
Prolactin and blood sodium	+0.43	n.s.
B. Animals adapted to fresh water 1–42 days		
Prolactin and body weight	—0.06	n.s.
Prolactin and blood sodium	—0.52	$p < 0.05$
C. Animals in the initial process of adapting to fresh water 30 min to 4½ hours.		
Prolactin and body weight	—0.92	$p < 0.001$
Prolactin and blood sodium	—0.87	$p < 0.001$
Blood sodium and body weight	+0.84	$p < 0.001$

TABLE 3

Partial correlation coefficients of pituitary prolactin content with other parameters in *Mugil cephalus* during the initial adaptation of fish to fresh water

Partial correlation between	Excluding	r	Significance
Prolactin and blood sodium	Time in fresh water	—0.922	$p < 0.001$
Prolactin and body weight	Time in fresh water	—0.918	$p < 0.001$
Prolactin and blood sodium	Weight	—0.459	n.s.
Prolactin and weight	Blood sodium	—0.695	$p < 0.02$

fish in the process of adapting to fresh water. No significant correlations were seen in sea water fish and only a relationship between prolactin and blood sodium was seen in fully fresh water adapted animals.

Blood sodium fell during the first 4.5 hours in fresh water (Table 1) and the effects of time were therefore separated from the correlation between prolactin and blood sodium in the group of fish adapting to fresh water by calculating partial correlation coefficients (Table 3).

The elimination of the effect of time has the effect of further increasing the signicance of the negative correlation between prolactin and blood sodium (Table 3). The inability to separate the correlation of prolactin with blood sodium from that with body weight is not surprising in view of the highly significant positive correlation between blood sodium and body weight during the initial stages of adaptation.

DISCUSSION

The present failure to demonstrate any apparent difference in mean levels of prolactin in the pituitaries of fish from sea water and those adapted to fresh water would at first seem to conflict with the previous demonstration of low prolactin levels in fish from sea and hypersaline waters (Blanc-Livni and Abraham, 1970). However the earlier work dealt with fish that probably had a long period of adap-

tation to their respective environments, whereas in the present work fish caught in sea water were migrating from the coastal bays where salinities of 20‰ are common. Further, Blanc-Livni and Abraham (1970) showed that although fish from fresh water transferred to sea water for 4 weeks had a reduced pituitary prolactin region, they were still more like fresh water fish than fish caught in the sea. The differences reported by Blanc-Livni and Abraham (1970) may therefore be the result of long term adaptations.

The present results concerned with the initial adaptation to fresh water show no striking change in absolute amounts of hormone, but instead show a significant and very rapid change in the correlation of the prolactin content of the pituitary with blood sodium levels, from no correlation in fish in sea water to a highly significant negative correlation in the initial period of adaptation to fresh water. A negative correlation between prolactin and body weight seen during adaptation disappears in fish after acclimatization to fresh water is complete; this relationship with weight seen during the period of adaptation is probably a consequence of the fact that larger fish have smaller surface area to weight ratios and therefore lose salts and gain water more slowly. This relationship between weight and blood sodium in these adapting fish is indicated by the significant positive correlation coefficient.

It is obviously possible that changes in prolactin synthesis and release rates may occur without corresponding change in the amount of hormone in the pituitary. It is however unlikely that changes in pituitary prolactin occur in the absence of a change in the relative rates of release and synthesis of hormones. The marked correlation that develops between prolactin and blood sodium when fish are placed in fresh water may be taken to indicate that changes in prolactin release rates occur in these initial stages of adaptation to fresh water. Work with other species of euryhaline fish indicate that prolactin is involved in adaptation to fresh water (Ball. 1969) and thus its rate of release probably increases when fish are transferred to fresh water.

The presence of a negative correlation between pituitary prolactin content and blood sodium in fish in fresh water does not, of course, give any indication of which comes first. the change in release of prolactin or the sodium level. Fish with lower pituitary prolactin contents may have released more hormone which by its effect in reducing permeability may have contributed to reducing sodium loss and account for the negative correlation.

In *in vitro* experiments with pituitaries of *Xiphophorus*, the release of material from prolactin cells increased with dilution of the culture medium (Sage, 1968), thus producing a positive correlation between pituitary prolactin content and the sodium concentration of the culture media. This is the opposite to what is observed *in vivo* in mullet. However, the *in vitro* experiments do not allow for other interactions that may occur in the intact animal. The other known mechanism for the control of prolactin release is by inhibitory activity of the hypothalamus (Sundararaj & Nayyar, 1969; Sage. 1970). Further work is required in order to determine the relative importance of neuronal and osmotic factors in the control of teleost prolactin cells.

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GALVESTON BAY BENTHIC COMMUNITY STRUCTURE AS AN INDICATOR OF WATER QUALITY

J. S. Holland, Nancy J. Maciolek and C. H. Oppenheimer

University of Texas Marine Science Institute, Port Aransas, Texas 78373

ABSTRACT

The objective of this study was to ascertain water quality through investigation of benthic community structure. Various methods of community structure analysis including several species diversity indices, rarefaction curves and a probability of interspecific encounter index were applied to data collected from selected sites in Galveston Bay, Texas. Hydrographic data and sediment analysis were used in interpreting the results of the various methods of investigating community structure.

The different methods of analysis used in this study showed very close agreement. It is suggested that three of the five investigation sites in Galveston Bay showed normal estuarine water quality. Two other stations showed evidence of large amounts of stress probably due to water quality. One of the two was probably stressed due to natural causes, primarily salinity fluctuations. The other, a channel site near a huge industrial complex, showed intermittent stress possibly due to man-made pollution.

INTRODUCTION

Galveston Bay is one of the most economically important and ecologically endangered estuaries on the Texas Gulf coast. Its economic importance stems from its proximity to one of the major population centers in Texas which depends on the bay for transportation of goods, waste disposal, cooling water, recreation and aesthetic appeal. Galveston Bay is also economically important as a major nursery and fishery area for commercially important estuarine and marine organisms. Unfortunately, these two uses of the bay tend to be mutually exclusive and the predominance of the former has brought about the question of the ecological status of Galveston Bay.

A great deal of significant estuarine research has been done in the Galveston Bay complex in the past decade. Several state universities (University of Texas, Texas A&M University), state agencies (Texas Water Quality Board) and federal agencies (National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service, and the Environmental Protection Agency (EPA)), have had major research programs which dealt directly with different ecological problems in Galveston Bay. The present study to determine seasonal and spatial variations in benthic communities was undertaken to augment water toxicity studies. Funding was provided through an interagency contract between the Texas Water Quality Board and The University of Texas.

It has been proposed (Wilhm and Dorris, 1968) that community structure of aquatic organisms may provide a better interpretation of water quality than standard physical and chemical analysis or toxicity studies. Hohn (1959) used diatom populations as a measure of water quality in selected areas of Galveston Bay. Bechtel and Copeland (1970) claimed that diversity indices calculated from numbers and weights of fish collected in Galveston Bay provided useful indicators of "environmental and pollution" stress.

Benthic fauna have been used in many studies of the relation between community structure and environmental stress, both natural and man-made. Boesch (1972) used Shannon's species diversity formula to investigate the structure of macrobenthic communities in marine and estuarine "soft mud" habitats. He found that diversity increased with depth offshore and decreased with naturally stressed and polluted estuarine areas. Sanders (1968) made a classic study of marine "soft bottom" fauna of different depths, latitudes, temperatures and salinities. He defined a diversity index known as the rarefaction method and proposed a stability-time hypothesis to explain community differences. Wilhm (1967, 1968, 1970) stresses the particular suitability of benthic macroinvertebrates for the study of water quality as their habitat preferences and low motility cause them to be directly affected by substances that enter their environment. He champions the use of diversity indices as associations or populations of benthic organisms are more reliable than singular "indicator" species. Diversity indices simplify the presentation of much data concerning numbers and kinds of organisms in a community.

These papers and many others (Wilhm and Dorris, 1966; Coull, 1972; Gage, 1972; Spence and Hynes, 1971 and Barnard, 1970 among the most recent) have indicated that benthic community structure may indeed be a useful indicator of water quality. The present study is an attempt to determine water quality at selected Galveston Bay sites through investigation of macrobenthic community structure.

AREA, METHODS AND MATERIALS

Description of Study Area

The Galveston Bay complex is the largest estuarine system on the Texas coast. It is comprised of several drowned river mouths and barrier island bays. Five sampling stations representing the broadest possible coverage of the bay were selected for this study (Fig. 1).

Two stations were chosen from the upper bay regions. Station 22, at the mouth of the Kemah Channel, is close to the Houston ship channel and this area might show effects from outflow of the Clear Lake region. Station 26, in Trinity Bay, is in an oil field area, very close to the mouth of the Trinity River and subject to great salinity variations relative to other bays in the complex but less variations than many other parts in Trinity Bay.

The study areas had basically two sediment types. Stations 17, 22 and 26 had predominantly soft mud bottoms with small amounts of shell fragments while Stations 14 and 29 had harder mud-shell sediments.

The difference in sediment types and position in the bay divided the stations into three types: lower bay, hard bottom; lower bay, soft bottom; and upper bay, soft bottom. In any investigation of the benthos, these differences, particularly the differences in sediment types, must be considered.

Field and Laboratory Methods

Benthic collections were made at the five stations in Galveston Bay (Fig. 1) in October, 1971;

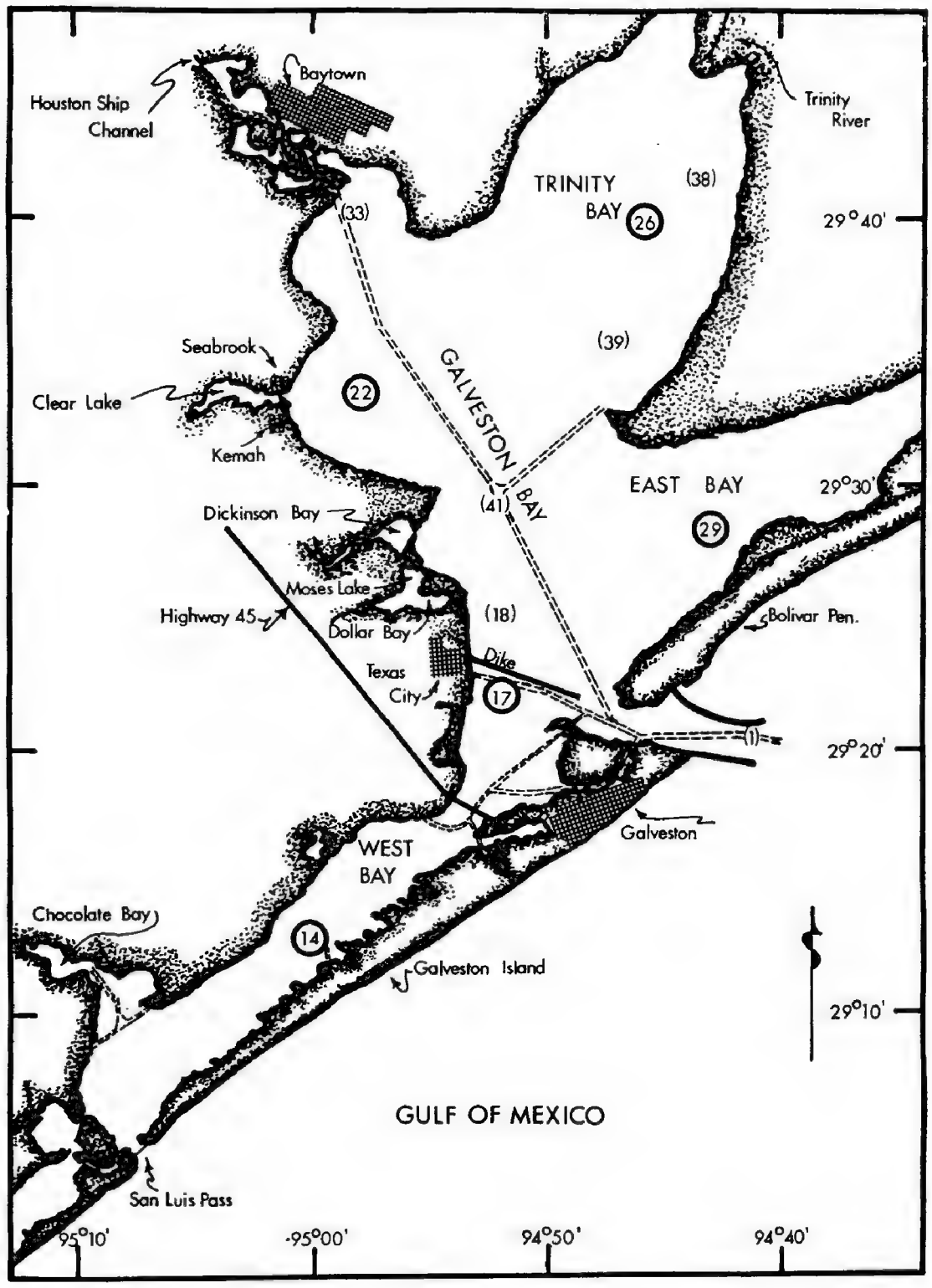

Figure 1. Location of Galveston Bay Sampling Sites

Three stations were located in the lower (seaward) portion of the bay. Station 14 in West Bay was selected on the hypothesis that its position, far from the major population areas and with openings to the Gulf at each end of the bay, would provide a "clean" site with the relatively stable conditions normally attributed to lower estuarine areas. Station 17, in the Texas City ship channel, was of interest for several reasons. It is at the confluence of several man-made channels, in an area most influenced by inflowing Gulf water and is possibly affected by the huge industrial complex in Texas City. Station 29 in East Bay was selected for the relative stability of its physical parameters and because water from the upper bay may have an effect on macrobenthos of this area.

January, April and July, 1972. Each sample was comprised of four grabs made with a modified Jackson controlled-depth, volumetric bottom sampler (Jackson, 1970). The sampler was chosen because depth of maximum penetration can be preset and the sample can be taken from a uniform depth (approximately 7 cm. in this study). The sampler covered an area of 25 × 18 cm. so that in four grabs approximately 12,600cc, or ½ cubic foot of sediment was collected. In the

harder sediment and shell of Stations 14 and 29, maximum penetration was not achieved on all grabs, consequently less sediment was obtained. Handles on the grab limited use to water of less than 14 ft. This affected only Station 17 when benthos collection were made just out of the channel. Field preservation of the samples varied slightly as better techniques were developed. The basic technique was to anesthetize the organisms in the sample with a 5% mixture of menthol crystals in 40% ethanol by adding the mixture directly to the sediment sample. The samples were later (4–6 hours) sieved in a graduated sieve box whose smallest mesh was 1.5 mm. All organisms retained by the screen were preserved in 70% alcohol (either ethanol or isopropanol). The preserved collections were sorted to species and identified. Counts of number of species and numbers of individuals per species were made.

Salinity, water temperature and dissolved oxygen were the major physical parameters recorded at each collection.

Data Interpretation Methods

Three methods of interpreting community structure were used:

I. Margalef (1956) proposed possibilities of analyzing natural communities through use of the information theory. Species diversity in natural communities may be equated with the uncertainty concerning the species of an individual drawn at random from the community. The more species in the community and the more evenly individuals are distributed, the greater the uncertainty of selecting one individual of a certain species, hence the greater the diversity. Information theory is a means of quantifying the amount of uncertainty which is then interpreted as a diversity. Pielou (1966a, 1967) gives an excellent explanation of the fundamentals of information theory as applied to biological communities.

A. The Shannon-Weaver diversity index provided one interpretation.

$$H' = -\sum_{i=1}^{s} P_i \log_e P_i \text{ natural bels/individuals}$$

The computational method used followed the use by Bechtel and Copeland (1970). Wilhm (1968) explains the use of H″ as an estimator of H′.

$$H'' = -\sum^{s} \frac{Ni}{N} \log_e \frac{Ni}{N} \text{ natural bels/individual}$$

The term natural bels/individual is used as natural logrithms were used in this formula (Pielou, 1966b). Calculations for H″ were programmed for a Monroe 1766 desk computer.

Our collections correspond to the Type B collections of Pielou (1966b) as they were considered to be representative of a larger parent population about which inferences were to be made. The basic assumptions involved in our use of Shannon-Weaver H′ are that all species found in the population will be represented in the sample and that parent population does indeed exist as a homogenous entity. The former assumption may present a weakness in this methodology.

B. Margalef's (1956) index for community diversity, D, was calculated:

$$D = \sum_{i=1}^{s} N_i \log_2 \frac{Ni}{N}$$

where D = community diversity, s = number of species, N_i = individuals in the species and N = total number of individuals.

The community diversity index D is closely related to numbers of individuals (sample size) and therefore is not useful in comparing the structures of unequally abundant communities. By dividing D by the number of individuals, an individual diversity index $\bar{d}$, which is not related to numbers of individuals, is obtained. The index $\bar{d}$ is then useful in comparing community structures using samples of differing sizes.

The theoretical maximum diversity (D_{max}) and minimum diversity (D_{min}) were calculated for each collection:

$$D_{max} = \log_2 N! - S \log_2 (\frac{N}{S})!$$

$$D_{min} = \log_2 N! - \log_2 N - (S\text{-}1)!$$

The calculation of D, D_{max} and D_{min} allows the calculation of redundancy, R, of a community. Redundancy may be approximated by several formulas using D_{max} and D_{min}. With small samples, such as our benthic samples, the following equation is most accurate.

$$R = \frac{\left[\sum_{i=1}^{s} \text{Log}_2 \, N_i! - X \, \text{Log} \, (N/S)! \right]}{[\text{Log}_2 \, (N - S + 1)! - S \, \text{Log} \, (N/S)!]}$$

D, $\bar{d}$ D_{max}, D_{min} and R were calculated on a 1106 UNIVAC computer by personnel of the Texas Water Development Board.

II. The Sander's rarefaction method is a method of allowing direct comparison of the numbers of species in samples by reducing (rarefying) them to a common size (Sanders, 1968). This methodology is limited to comparison of communities in similar habitats and to use only on similar groups of organisms. The normal application is to specified fractions of a community (the polychaete-bivalve fraction was used in the present study). This method has been used by Gage (1972) for macrobenthos studies and Coull (1972) for analyses of species diversity of meiobenthic copepods of the deep sea.

III. The "probability of interspecific encounter" method, according to its author (Hurlbert, 1971), is not a species diversity index.

$$\Delta_1 = \left(\frac{N}{N-1}\right) \left(1 - \sum_{i=1}^{s} \left(\frac{Ni}{N}\right)^2\right)$$

where N_i = number of individuals in the ith species and N = total number of individuals. Δ_1 (P.I.E.) is the probability that an encounter between two members of a community will be interspecific. Or, if an organism from outside the community (biologist, etc.) encounters at random two organisms in the community, Δ_1 is the probability that they will be of different species. P.I.E. values may be valid indicators of water quality. Hurlbert (1971) states that communities with high P.I.E. values are comprised of organisms which can tolerate few random components in their interaction with their environment. Sanders (1968) describes the same sort of community as predominantly biologically controlled or lacking in physical stress. It follows then that stressed areas should be characterized by communities with low P.I.E. values. Hurlbert (1971) states that communities having different species composition are not intrinsically arrangeable in linear order on a diversity scale and that P.I.E. values were not intended as a new diversity index. Use of P.I.E. in this study is based on the hypothesis that probability of interspecific encounter may be a measure of stress in estuarine macrobenthis communities.

RESULTS

Sampling of the macrobenthos at five stations in Galveston Bay resulted in the collection of 9381 individuals comprising 127 species (Table 1). Almost two-thirds of the individuals were of one species of barnacle, *Balanus eburneus*. The dominant taxocenes were polychaetes, bivalves and crustaceans. Individuals from ten other taxocenes were collected.

Fifty-nine species of polychaetes were collected. Polychaetes were found at all stations but were common in lower bay stations and noticeably scarce at Station 26 in Trinity Bay. Polychaetes were not collected at this station in October and were represented by only one species, *Nereis succinea*, in April and July. The January collection at Station 26 had small numbers of seven polychaete species. It seems apparent (Table 1) that the polychaete fraction of the samples was variable through the year. The first and last collections at all stations appear to have both fewer species and numbers of polychaetes. Analysis of variance of H″ and P.I.E. values (Table 4 for P.I.E.) did not indicate significant differences

TABLE 1

List of species and abundances in samples taken at 5 Galveston Bay stations

(Collection dates are: 1-October, 1971; 2-January, 1972; 3-April, 1972; 4-July, 1972; 4a-August, 1972)

Phylum	Class	Species	Station 14				Station 17				Station 22				Station 26				Station 29			
			1	2	3	4a	1	2	3	4a	1	2	3	4	1	2	3	4	1	2	3	4
Coelenterata:		*Cerianthes* sp. (?)	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Rhyncocoela:		Nemerteans	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	4	4	..	..
Nematoda:		Nematodes	..	1	..	..	..	1	..	..	..	11	..	..	..	..	..	..	..	..	..	..
Annelida:	Polychaeta:	*Lepidonotus sublevis*	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Lepidasthenia commensalis	..	..	5	1	..	..	..	..	.	..	..	..	..	..	..	..	3	14	7	..
		Polynoid A.	..	..	..	..	..	..	..	..	..	..	..	..	....	..	..	..	1	..	..	..
		Sthenelais boa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..
		"Scaleworm"	..	..	..	..	..	..	..	..	..	..	..	..	....	..	..	..	1	..	..	..
		Pseudeurythoe ambigua	..	..	..	..	..	..	..	..	..	..	..	..	..	.	..	..	..	..	1	..
		Amphinomid A.	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
		Eumidea sanguinea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	57	..	..
		Nereiphylla fragilis	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..
		Gyptis vittata	..	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	5	..	..
		Ancistrosyllis jonesi	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
		Parandalia fauveli	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	2	..	..
		Typosyllis corallicoloides	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..
		Syllis cf. corallicoloides	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..
		Nereis succinea	..	9	13	1	..	7	2	..	..	..	74	11	..	3	60	6	7	93	42	14
		Ceratonereis irritabilis	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Laonereis culveri	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..
		Glycera americana	..	2	9	1	4	7	2	..	..	..	..	2	..	..	..	..	..	..	..	..
		Glycinde solitaria	..	..	..	..	..	3	..	..	..	2	2	..	..	..	..	..	..	..	..	..
		Diopatra cuprea	..	1	1	..	13	9	..	..	2	..	..	..	..	..	..	..	..	..	1	..
		Marphysa sanquinea	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..
		Lumbrinereis parvapedata	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Lumbrinereid A.	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
		Drilonereis magna	..	5	1	2	..	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..
		Stauronereis rudolphi	..	1	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Dorviellid A.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
		Aricidea jefferysi	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Aricidea sp.	..	..	1	..	..	.	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Streblospio benedicti	..	1	..	..	..	328	1	..	..	1	..	..	..	1	..	..	..	5	..	..
		Prionospio pinnata	..	..	..	..	..	6	1	..	..	14	..	..	..	5	..	..	..	..	..	..
		Polydora ciliata	..	..	..	..	..	5	..	..	..	..	.	..	..	..	..	..	..	..	..	..
		Polydora socialis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..

		Tharyx setigera	..	..	3	3	..	..	1	.	..	..	..	..	.	..	..	..	..	..	..	..	..	..
		Notomastus hemipodus	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Mediomastus californiensis	..	7	..	..	..	3	..	.	.	4	..	..	..	1	..	..	..	57	..	..	..	..
		Heteromastus filiformis	..	..	..	..	..	14	3	..	..	.	2	..	..	..	..	..	..	..	..	..	..	..
		Heteromastus elongata	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..
		Clymenella torquata calida	..	4	15	..	..	..	..	.	..	..	..	..	..	..	..	..	..	1	..	..	..	..
		Clymenella mucosa	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Branchioasychis americana	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Maldanid A.	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Pectinaria gouldi	..	..	..	..	..	..	..	.	.	2	2	..	..	..	..	..	..	..	..	..	..	..
		Melinna maculata	..	1	47	5	..	2	9	..	..	..	..	..	..	..	..	..	..	..	..	10	..	..
		Amphictis gunneri floridus	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	1	..	..	..	..
		Ampharetidae or Terebellidae	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
		Pista palmata	..	26	..	..	..	..	..	..	..	..	..	..	..	..	..	..	57	..	..	..	..	..
		Pista sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	196	70	..	..	..
		Eupolymnia crassicornis	..	..	253	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Chone duneri	..	3	..	..	..	..	..	.	..	.	..	..	..	..	..	..	..	..	..	..	..	..
		Megalomma bioculatum	..	3	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Sabella melanostigma	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Sabella micropthalma	..	5	..	..	..	..	..	..	..	..	..	..	.	..	..	..	..	..	..	..	..	..
		Sabellid A.	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Sabellid or Serpulid	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
		Eupomatus dianthus	..	1	21	2	..	..	..	..	..	..	..	..	..	31	..	..	..	54	7	..	..	..
		Hypaniola gunneri floridus	..	1	..	..	..	.	..	..	..	..	.	..	..	..	..	..	..	..	..	..	..	..
		Ehlersileanura incisa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..	..
		Unidentified worm "X"	..	..	1	..	..	..	..	..	.	..	.	..	..	..	..	..	..	..	..	..	..	..
		Unidentified worm "Y"	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Oligochaeta:		..	1	..	..	..	..	..	..	..	.	..	..	..	..	..	..	..	..	..	..	..	..
Mollusca:	Gastropoda:	*Littoridina sphinctostoma*	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	..	..	..	..	..	..
		Crepidula plana	..	2	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	9	..	..	..	..
		Crepidula fornicata	..	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..
		Crepidula sp. (?)	..	..	..	..	..	..	..	..	..	..	1	..	.	..	..	..	1	..	..	..	..	..
		Thais haemostoma	..	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Anachis obesa	..	..	..	1	..	..	..	..	..	.	..	1	..	..	1	..	42	13	..	28	..	..
		Anachis avara	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..
		Turbonilla (*interrupta* ?)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..	..
		Pyramidella crenulata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
	Bivalvia:	*Nuculana concentrica*	..	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Anadara transversa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	1	..	1	..	..
		Amygdalum sp.	..	..	1	..	..	..	..	..	..	..	1	7	..	..	..	..	..	..	1	1	..	..
		Modiolus demissus	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
		Brachidontes exustus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..	..
		Ostrea equestris	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Crassostrea virginica	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..

Phylum	Class	Species	Station 14				Station 17				Station 22				Station 26				Station 29			
			1	2	3	4a	1	2	3	4a	1	2	3	4	1	2	3	4	1	2	3	4
		Aligena texasiana	..	..	35	..	..	..	..	..	.	..	..	..	..	..	..	..	..	..	..	..
		Laevicardium mortoni	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Mulinia lateralis	..	21	28	..	..	1	..	..	..	1	9	1	95	..	..	1	..	..	..	..
		Rangia flexuosa	..	..	..	..	..	..	..	..	..	.	..	..	49	.	1	1	..	..	..	..
		Rangia cuneata	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..	..	..
		Ensis minor	..	..	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
		Macoma mitchelli	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..
		Macoma brevifrons	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Tellina aequistriata	..	..	12	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Tagelus divisus	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Abra aequalis	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Cumingia tellinoides	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	8	4	1
		Cyclinella tenuis	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Congeria leucophaeta	..	..	..	..	..	1	..	..	..	..	..	1	..	..	4	1	..	..	..	..
		Mercenaria c. texana	..	1	2	1	..	..	..	..	..	.	..	..	..	..	..	..	..	..	..	..
		Diplothyra smythi	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	4	..	1
		Barnea truncata	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
		Lyonsia hyalina floridana	..	28	203	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Arthropoda:	Pcynogonida:		..	1	2	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
	Crustacea:	*Balanus eburneus*	..	..	7	..	..	..	40	.	..	..	121	13	..	..	4711	1470	..	39	..	7
		Cassidinidea lunifrons	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	13	..	..	..	..
		Ampithoe sp.	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Ampelisca abdita	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Corophium louisianum	..	1	..	..	..	..	..	..	..	..	..	..	..	..	4	3	..	..	..	..
		Melita sp.	..	3	1	..	..	..	..	..	..	..	6	26	..	..	..	51	2	20	..	8
		Amphipod "A"	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..
		Amphipod "B"	..	..	1	..	..	..	..	..	..	..	.	..	..	..	..	..	1	..	..	..
		Pinnixia retinens	..	..	1	..	1	..	..	..	..	..	2	4	..	..	..	..	24	25	8	26
		Hepatus pudibundus	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Panopeus herbstii	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..
		Panopeus sp.	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
		Clibanarius vittatus	..	..	..	..	..	..	1	..	..	..	..	..	..	.	..	..	..	..	..	..
		Rhithropanopeus harrisii	..	..	..	..	..	..	..	..	..	..	..	8	..	..	..	7	..	..	..	1
		Petrolisthes armatus	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	4	1	12	..	5
		Hexapanopeus augustifrons	..	..	..	..	..	..	..	..	..	..	.	..	..	..	..	..	..	1	..	..

		Eurypanopeus depressus	..	..	..	..	..	..	..	.	..	..	..	..	..	..	..	..	..	..	1	2
		Neopanope t. sayi	..	..	..	..	..	..	..	..	..	..	.	1	..	..	8	4	..	..	1	..
		Unidentified crab "A"	..	..	..	..	..	.	..	.	..	.	..	..	..	..	..	2	..	..	..	..
		Unidentified crab "B"	..	..	..	..	..	.	..	..	.	..	..	..	..	..	..	1	..	..	..	..
		Unidentified xanthids	..	..	..	..	..	..	..	..	..	.	..	..	.	.	..	..	..	..	..	4
		Neopanope texana texana	..	..	..	..	..	..	..	.	..	..	..	..	..	..	..	..	..	..	..	1
Sipunculida:		*Phascolion strombi*	..	..	2	..	..	..	..	.	..	..	..	..	..	..	..	..	..	..	..	..
Phoronida:		*Phoronis architecta* (?)	..	..	..	..	..	1	..	..	..	2	..	..	..	7	..	..	..	..	..	..
Echinodermata:	Ophiuroidea:	*Micropholis atra*	3	6	6	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
		Hemipholis elongata	..	..	..	..	..	.	1	..	..	..	..	..	..	.	..	..	1	..	..	..
	Holothuroidea:	Cucumerid	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chordata:	Ascidiacea:	*Mogula manhattensis* (?)	..	..	..	..	..	1	..	..	..	..	..	..	.	..	..	..	..	..	..	..
	Pisces:	*Myrophis punctatus*	..	.	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..

in benthic populations through time. Analysis of H″ values computed for polychaetes only indicated no significant variation in that fraction of the community through time.

Twenty-five species of bivalves were collected. No pattern in the general distribution of bivalves through time was apparent. Bivalves were least diverse at Stations 17 and 26 although large numbers of several species were collected at Station 26 in October. Station 14 showed the greatest diversity of bivalves.

Twenty-two species of crustaceans were collected. The population explosion of *B. eburneus* at Station 26 in April and July made crustaceans far outnumber all other taxocenes. As with bivalves, no particular distribution pattern through time was observed. Some peculiarities in crustacean spacial distribution were noted. Station 14 almost lacked decapod crustaceans, while the other mud-shell sediment station, 29, had more crabs than any other station. All stations except 29 show maximum numbers of the barnacle, *B. eburneus*, in April. Isopods were collected only at Station 26. Amphipods appeared in the upper bay stations only in the last two collections.

Only four species, *Nereis succinea, Streblospio benedicti, Mediomastus californiensis*, and *Balanus eburneus* were found at all five stations. Five other species, *Diopatra cuprea, Anachis obesa, Mulinia lateralis, Panopeus herbstii* and *Melita* sp. were each found at four stations. All other species were collected at three stations or less.

The ephemeral nature of the contribution to community structure of some species was noted at many stations. Isopods were found at Station 26 only during the July collection. No barnacles were found at Station 26 in the first two collections but a total of over 6000 were taken in the last two collections. A few *Lyonsia hyalina floridana* were collected at Station 14 in January, while over

TABLE 2

H″ values

	14	17	22	26	29
October	1.8222	0.7298	1.0397	0.7277	1.7700
January	2.9698	0.9443	1.7158	1.5296	2.3919
April	2.0043	1.8033	1.2778	0.0970	1.9033
July	2.5406	0	2.1336	0.3914	2.0032
$\bar{x}$	2.3347	0.8693	1.5417	0.6864	2.0171

TABLE 3

P.I.E. values

	14	17	22	26	29
October	0.9644	0.4509	0.8333	0.4740	0.7557
January	0.9203	0.3253	0.7795	0.6505	0.8552
April	0.7686	0.6772	0.6060	0.0321	0.7617
July	0.9338	0	0.8460	0.1364	0.8262
$\bar{x}$	0.8967	0.3633	0.7662	0.3232	0.7997

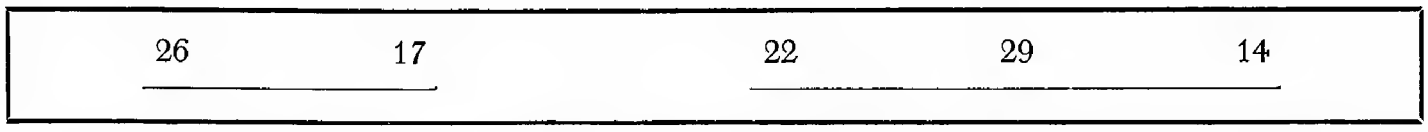

FIG. 2. Duncan's New Multiple Range Test of P.I.E. values. Groups of stations underlined by the same line were not significantly different.

200 were collected at Station 14 in April and none in July. It is apparent that many species either fluctuate widely in abundance or change their habitat preference so as to become less available to the sampling procedures used.

The complexity of community structure when observed in terms of numbers of species, numbers of individuals and varying patterns of distribution invites some quantitative methods of comparison among communities. Analysis of the present data by three different methods gave similar results.

H″ values for the samples from various stations were computed (Table 2). October values for Station 14 for both H″ and P.I.E. computations are replacement values following the method of Snedecor and Cochran (1967) for replacement of a single missing value in randomized blocks design analysis of variance. This was necessary because this collection dried out in a defective container. The H″ value of zero at Station 17 in July reflects the lack of organisms found in that collection. This sample was recollected in mid-August and the lack of organisms at Station 17 was confirmed.

Values of D, $\bar{d}$, D_{max}, D_{min} and R for all collections are given in Table 5. D and $\bar{d}$ values calculated with $\log_2$ and $\log_e$ are given. The $\bar{d}$ values based on $\log_e$ are the same as H″ values (Table 2). Note that the d $\log_2$ values are approximately 1.44 times as large as the d $\log_e$ values. The zero values found in both tables for Station 14, collection 1 indicate that this data was lost and not replaced as previously noted for the H″ values.

Probability of interspecific encounter (P.I.E.) values were calculated (Table 3). Low values in April and July at Station 26 are evident in both these and the H″ values. The lack of organisms at Station 17 in July is again reflected.

Variation of community structure through time and space was analyzed by an analysis of variance of both H″ and P.I.E. values. (Table 4 for P.I.E. analysis). Both tests showed significant variations between stations but no significant differences between seasonal collections. Duncan's new multiple range test (Li, 1966) was performed on P.I.E. data (Fig. 2). A sharp distinction was obtained

TABLE 4

Analysis of variance of P.I.E. values

Source of variation	Degree of freedom	Sum of squares	Mean squares	F
Total	19	1.69072		
Between seasons	3	0.10227	0.03409	0.90174n.s.
Between treatments	4	1.13475	0.28368	7.50358**
Error	12	.45368	0.3780	

n.s. = not significant.
** = significant at 1% level.

TABLE 5

Diversity indices D, $\bar{d}$, D_{max}, D_{min} and Redundancy. Values for each station by collection. D and $\bar{d}$ values for both Log_2 and Log_e

		Log_2					Log_e	
Station	Coll.	Diversity	$\bar{d}$	D_{max}	D_{min}	Redundancy	Diversity	$\bar{d}$
14	1	0	0	0	0	0	0	0
14	2	698.457	4.285	788.943	272.513	0.315	484.089	2.970
14	3	2001.197	2.900	3441.268	310.111	0.484	1386.996	2.010
14	4	102.641	3.666	97.953	65.414	0.566	71.139	2.541
17	1	18.955	1.053	24.034	8.258	0.548	13.137	0.730
17	2	545.041	1.363	1694.400	172.196	0.782	377.759	0.944
17	3	187.336	2.602	262.268	101.937	0.642	129.839	1.803
17	4	0	0	0	0	0	0	0
22	1	6.001	1.500	4.585	3.585	1.000	4.159	1.040
22	2	94.073	2.476	107.297	40.846	0.420	65.201	1.716
22	3	416.678	1.844	842.872	108.900	0.618	288.792	1.278
22	4	255.520	3.079	310.324	87.583	0.371	177.097	2.134
26	1	154.354	1.050	225.530	14.391	0.365	106.980	0.728
26	2	119.179	2.207	186.646	56.274	0.652	82.601	1.530
26	3	670.847	0.140	13419.641	73.354	0.956	464.953	.097
26	4	894.089	0.565	6175.239	148.728	0.882	619.675	0.391
29	1	385.637	2.554	620.068	114.637	0.526	267.279	1.770
29	2	2208.692	3.451	3090.955	250.912	0.336	1530.808	2.392
29	3	466.861	2.746	648.981	117.510	0.409	323.574	1.903
29	4	289.031	2.890	352.608	85.203	0.339	200.322	2.003

indicating that Stations 17 and 26 were different from Stations 14, 22 and 29.

Rarefaction methodology (Sanders, 1968) was used to generate "species diversity" curves (species richness curves following Hurlbert's terminology) for each collection (Fig. 3). These curves were based on the polychaete-bivalve fraction of each collection. Many of the curves are abruptly truncated due to the small numbers of organisms collected at the various stations.

Examination of the rarefaction species richness curves indicates that species richness was not decidedly different between Stations 14, 22 and 29. Stations 14 and 29 had the greatest numbers of individuals and thus the most complete curves. The initial slopes of these curves are very similar to those found at Station 22. Species richness curves for Stations 17 and 26 indicate some differences. At Station 17, collections 2 and 3 follow the general curve indicated at other stations. The curve for the first collection at this station is decidedly lower than the general pattern at other stations and no curve could be generated for the fourth collection as only one organism was collected. At Station 26, collections 2 and 4 apparently follow the generalized pattern of Stations 14, 22 and 29 but collections 1 and 3, though containing more individuals, show a different species richness.

DISCUSSION

It has been observed (Johnson, 1970; Sanders, 1968; Boesch, 1972) that

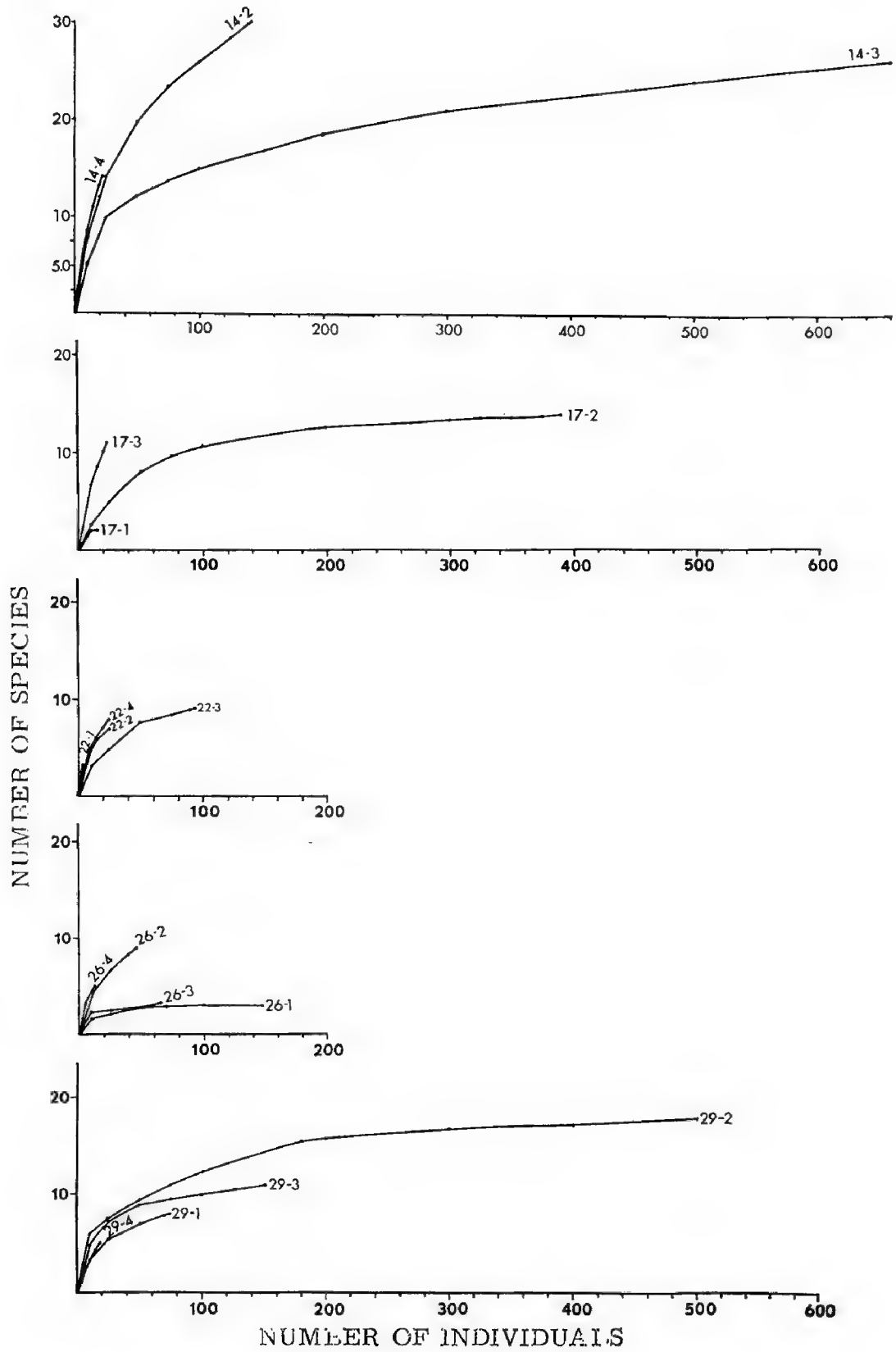

Figure 3. Rarefaction curves of polychaete-bivalve fraction of benthos collections from Galveston Bay. Numbers on lines indicate station and collection number.

heterogeneity of physical environment is a major factor influencing differences in benthic community structure. Boesch (1972) documented benthic diversity differences through an estuarine system to the continental shelf. Diversity was highest on the shelf and decreased with distance up the estuary. Sanders (1968) explains this variation with his stability-time hypothesis. With the exception of Station 17, a similar gradient occurred in Galveston Bay. Heterogenous sediment types also influence variance in benthic species diversity. Gage (1972) found

more diverse communities in muddy sand than in soft mud. No real analysis of the sediment types at the different stations was attempted but our description of the sediments agrees with that of Bechtel (1970) who used the same stations. Stations 14 and 29 had much firmer mud with large quantities of shell and the most diverse communities. The other stations had soft mud bottoms and lower diversity values, except Station 22, which was more similar in diversity to the lower bay stations (14 and 29). Duncan's new multiple range test (Fig. 2) and Sanders' rarefaction curves (Fig. 3) indicate this similarity. Mean P.I.E. and H″ values (Tables 2 and 3) for Station 22 are only slightly lower than those of Stations 14 and 29.

The three basic methods of data analysis appeared to be compatible. Several authors have applied different indices to their data to compare effects (Menhinick, 1964; Wilhm, 1967). Coull (1972) applied several indices in his study but reported only the rarefaction analysis. The present debate (Hurlbert, 1971) concerning the validity of species diversity indices prompted the use of several methodologies of investigating community structure. The Shannon-Weaver and Margalef indices are similar species diversity indices based upon information theory. The Shannon-Weaver H′ index was computed using $\log_e$ while the Margalef functions D, d, and R used $\log_2$.

No reports were found which contained either H′ or $\bar{d}$ values for estaurine macrobenthic communities. Wilhm (1967, 1968, 1970) has done a great deal of work on fresh-water macrobenthos using several indices. Bechtel and Copeland (1970) indicate that the guidelines proposed by Wilhm and Dorris (1968) for biological interpretation of water quality may be used for estuarine fish studies. Their guideline, based on $\bar{d}$, states that index value less than one indicate heavy pollution, values between one and three indicate moderate pollution, and values above three indicate no pollution. These values are probably too high for estuarine community studies. Wilhm and Dorris (1968) were working with stream macrobenthic communities and using $\bar{d}$ as their species diversity index. Bechtel and Copeland (1970) worked with estaurine communities and used the diversity index H′. The estuarine communities, under non-polluted conditions, would be subject to greater natural stresses than those in an unpolluted stream and consequently should show lower diversity index values. A second objection to Bechtel and Copeland's comparison of their data to that of Wilhm and Dorris is in the comparison of H′ to $\bar{d}$ values. The H′ statistic used by Bechtel and Copeland uses $\log_e$ in its calculation while $\log_2$ is used by Wilhm and Dorris in computing $\bar{d}$. An H′ value as calculated by Bechtel and Copeland has to be multiplied by approximately 1.44 to convert it into a $\bar{d}$ value. Thus it appears that the index values used by Bechtel and Copeland were only approximately two-thirds of the value of those used by Wilhm and Dorris. If their data did follow the guidelines as proposed by Wilhm and Dorris, it appears to be the fortuitous result of mistakenly using H′ to compare with $\bar{d}$. As both H′ and $\bar{d}$ were calculated for the present study, it is felt that H′ values of macrobenthic communities above 2.0 and $\bar{d}$ values above 2.5 indicate areas of normal estuarine stress (clean estuarine water). It is difficult to define a clear cut range of values in dealing with estuarine

communities. Quite possibly, we should define "lower estuarine stress" as the set of normal conditions found in the most stable, seaward portion of the estuary and simply place a single value on clean lower estuary water. We can then acknowledge that lower values indicate areas of greater than "lower estuarine stress". The cause of the stress, be it pollution or natural stress, cannot be determined from the index value. A value indicating clean, lower estuarine water would vary between estuaries but should remain similar.

The second of the three basic methods for analyzing community structure was Sanders' rarefaction methodology. It is not a diversity index that attaches a specific number to a given community. It allows the rarefaction (making smaller) of a larger community (sample) to compare the number of species taken to that which would have been taken if a smaller number of individuals had been collected. It is, then, a direct method of comparing species richness between communities. Curves generated for our "higher diversity" stations agree closely with those of Sanders (1968) for a tropical estuary. Our curves showed almost identical diversity to those of Sanders although his were made on soft mud communities. The soft mud communities should show lower diversities (Gage, 1972). We believe the similarity of the curves to be due to the difference in latitude between his tropical estuaries and Galveston Bay. The similarity of these curves points out the "naturalness" of the high diversity stations we observed, assuming that the tropical estuaries observed by Sanders were unpolluted.

The third method for analyzing community structure was proposed by Hurlbert (1971). Hurlbert is highly critical of species diversity as a concept and provides several biologically oriented alternatives. His "probability of interspecific encounter" (P.I.E.) is one used in this study. In his description of the biological significance of P.I.E., Hurlbert describes the low stress, highly biologically adapted community as having high P.I.E. values. He says that this type of community can tolerate little randomness in its search for mates, food or hosts, noting that the most random method of plant "mate-seeking", wind dispersal of pollen, is essentially absent from high P.I.E. communities such as rain forests. The converse should also be true: communities which are highly stressed, showing great randomness in their search for food, mates or hosts, should show low P.I.E. values. In an estuarine situation, with the great variation in natural stress, it was hypothesized that macrobenthic community P.I.E. values might indicate water quality.

All of our data analysis methods appear to give similar results. The rarefaction curves agree very closely with the H″, $\bar{d}$ and P.I.E. values.

Our data indicate that Stations 14, 22 and 29 are generally areas of normal estuarine stress. The rarefaction curves generally agree with those of Sanders, as previously mentioned and the H″, $\bar{d}$ and P.I.E. values are high. Stations 17 and 26 are definitely areas of greater stress. Analysis of variance of both P.I.E. and H″ values indicated differences between the stations. Duncan's new multiple range test (Fig. 2) shows the differences clearly as do the rarefaction curves.

The greater stress at Stations 17 and 26 apparently is periodical. At Station 17, collections taken in the cooler months (January and April) appear to be close to the average species diversity of the other stations. Those collections made in

months when the water temperature was high (July and October) show definite diminution of diversity. At Station 26, the January collection showed H″, $\bar{d}$ and P.I.E. values similar to the "high diversity" stations. October values for this station were similar to those at Station 17 while the indices for April and July were very low due to the dominance of the barnacle, *B. eburneus*. The redundancy, R, clearly demonstrates the dominance of the barnacle in both of these collections. Rarefaction curves for Station 26, which do not take the explosion of the barnacle population into account, indicate that the species richness during January and possibly July was similar to that of the "higher diversity" stations. Species richness during October and April was severely diminished. Salinity at Station 26 in January was very low (circa 3‰, Fig. 4). At first glance, one tends to interpret the abundance of species at this time and lack at all other times as an ill effect of high salinity upon this community. This does not seem to be the case as a close inspection of Table 1 shows that most of the organisms collected at Station 26 in January were polychaetes which were found at higher salinities at other stations. This was the only collection at Station 26 in which polychaetes were prevalent. Several of the polychaete species found at this time were also found in large numbers at other stations. The high diversity at Station 26 in January is possibly due to the annual reproduction cycle of certain euryhaline polychaete species in Galveston Bay.

This fluctuation in polychaete species numbers and individuals for most sta-

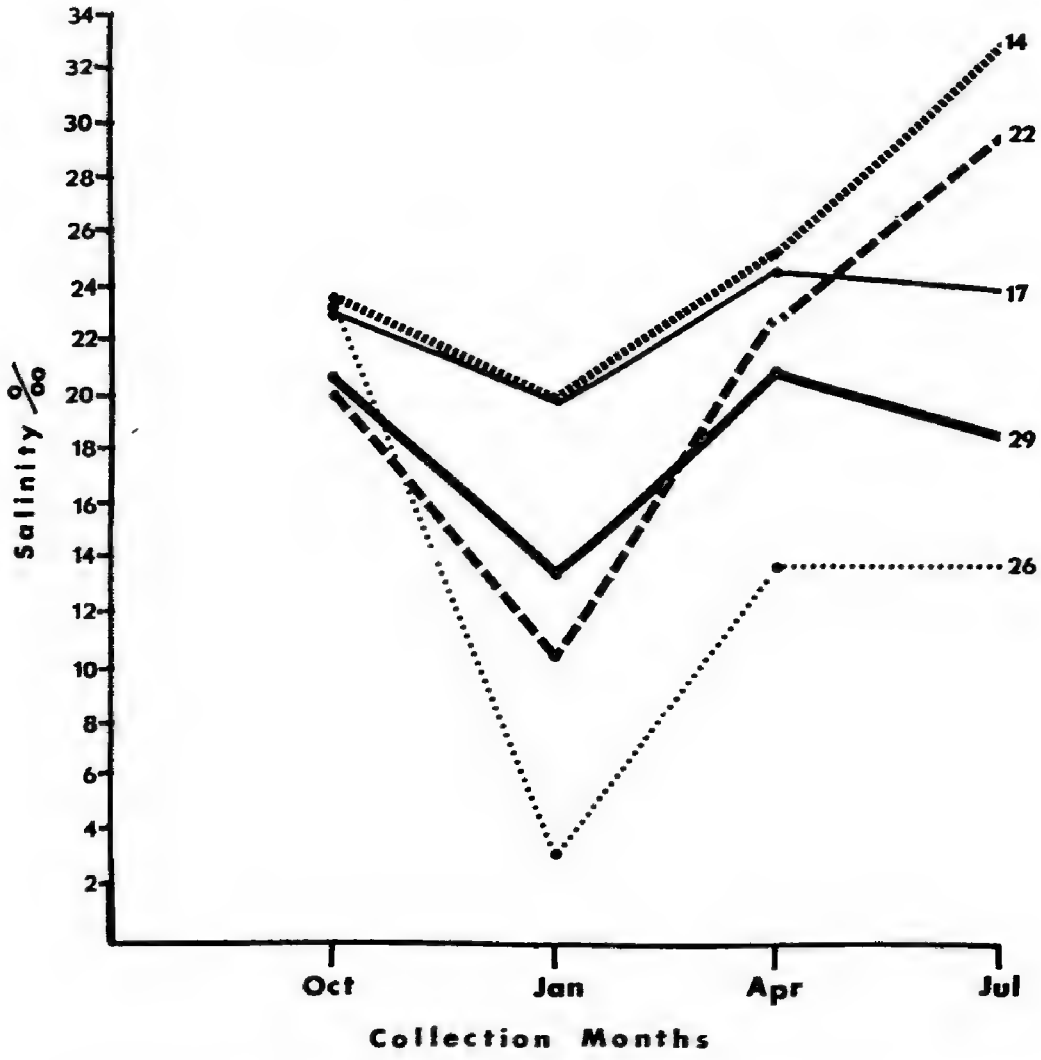

Figure 4. Mean Bottom Salinities at Galveston Bay Sampling Sites

tions is apparent in Table 1 but was not shown to be significant by analysis of variance of either P.I.E. or H″ values. Variance among seasonal samples was analyzed by Bartlett's test and was found to be homogenous. The reason for the statistical nonsignificance of the apparent fluctuation is believed to be a function of the mathematical treatment of numbers of species and individuals to give index numbers but the exact reason is not known. The fluctuation in numbers of polychaete individuals collected seasonally is believed to be real.

It is felt that the existence of greater than normal stress at Stations 17 and 26 is indicated by the macrobenthic communities at these stations. Examination of all physical parameters existing at these sites indicates that the stress at Station 26 is probably primarily natural stress. The station is only about five miles from the mouth of the Trinity River and is probably subjected to the maximum "natural" stress of temperature and salinity to be found in the Galveston Bay complex. The analysis of heavy metals in the sediment at Station 26 (Table 6) shows no unusually high concentrations. Arsenic (2.6 ppm.) was the only heavy metal at this station that was high relative to the other sampling sites. Hann and Slowey (1972) state that coastal sediments have an average of 3 ppm. arsenic. Arsenic is found in concentrations of 3–15 ppm. in deep sea sediments (I.D.O.E., 1972), so that the observed arsenic levels in Galveston Bay are not thought to be limiting. Pesticide analysis (Table 7) indicates only traces of two pesticides at Station 26. There does not appear to be any man-made cause for the low diversity structure of the macrobenthos at Station 26.

The stress indicated at Station 17 is possibly due to pollution. This station is low enough in the bay to have a very stable temperature-salinity regime. Its salinity shows the least variation of the sites sampled. It is a relatively deep station so that temperature changes should be moderated. Our collections were made out of the main channel due to depth restriction on our sampler. Channel dredging should have had little effect on the benthic community at our collection site. All physical parameters available to us were investigated. None showed evidence of causing the low values encountered. Concentration of heavy metals in the sediment of this station are consistently either the highest or second highest of all stations sampled. It is not known that the observed concentrations of metals are toxic but the consistently high concentrations are believed to be indicative of a large amount of pollution, probably from the Texas City industrial complex. The sediment heavy metals analysis at this site was made by Hann and Slowey (used

TABLE 6

Concentration of selected heavy metals in Galveston Bay sediment*

Station	Depth (in.)	As ppm	Ba ppm	Cr ppm	Cu ppm	Fe ppt	Pb ppm	Mn ppm	Hg ppb	Ni ppm	Zn ppm
14	0–6	1.4	16	14	8.9	8.4	19	212	56	11	52
17	0–6	3.4	61	89	36	12.7	48	727	111	33	122
22	0–6	1.9	93	50	80	8.0	39	630	114	57	83
26	0–6	2.6	36	25	10	6.8	19	234	53	21	42
29	0–6	1.4	15	24	5.1	5.2	9	260	28	17	32

* Used with permission from Hann & Slowey, 1972.

TABLE 7

Pesticide analysis of Galveston Bay Stations*

	PPB														
Station	α-BHC	B-BHC	Lindane	Hepta-chlor	Heptachlor epoxide	Dieldrin	Aldrin	Endrin	P,P' DDE	O,P' DDD	P,P' DDD	O,P' DDT	P,P' DDT	Kelthane	Chlordane
14	P	....	P	....	....	....	....	....	0.45	....	....	....	....	....	....
17	0.42	0.66	....	....	....	....	....	....	....	....	....	....	....	....	....
22	0.22	....	0.69	0.16	....	P	....	P	P	P	....	....	....	P	....
26	P	....	P	....	....	....	....	....	....	....	....	....	....	....	....
29	0.49	....	2.63	2.63	....	....	....	P	....	P	P	P	P	....	....

P = trace
* Used with permission from Hann & Slowey, 1972.

with their permission), in July 1972. This was just prior to the final benthos collection in which no living organisms were found. The apparent seasonality of the low diversity values may be due to greater or different pollution during the warmer months or to a temperature interaction affecting the toxicity of the pollutants. Periodic occurrence of low DO values have been suggested as a possible cause of the observed low diversities at this station. However, no low O_2 values were observed during the sampling periods. Further investigation of the benthic communities in the Texas City channel and the pollution abatement control of the Texas City industrial complex is indicated.

CONCLUSIONS

I. Water quality in Galveston Bay based on benthic macroinvertebrate communities is good in most areas sampled.

II. Benthic macroinvertebrate community structure indicates that Station 26, in Trinity Bay, is highly stressed. This is thought to be due to natural causes.

III. Station 17, in the Texas City ship channel, is the only station sampled that indicates probable effects of man-made stress (pollution). Possible water temperature-toxicity interaction or more damaging pollution during summer months may be occurring at this station.

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